The effects of model structure and complexity on the behaviour and performance of marine ecosystem models.

by

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Declarations

Originality

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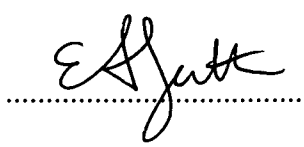

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Abstract

Despite increasing use of ecosystem models, the effects of model structure and formulation detail on the performance of these models is largely unknown. Two biogeochemical marine ecosystem models were constructed as the foundation of a study considering many aspects of model simplification. The models use a trophic web that is resolved to the level of functional groups (feeding guilds), and includes the main pelagic and benthic guilds from primary producers to high-level predators. Both models are process based, but the Integrated Generic Bay Ecosystem Model (IGBEM) is highly physiologically detailed, while Bay Model 2 (BM2) uses simpler general assimilation equations. Both models compare well with real systems under a wide range of eutrophication and fishing schemes. They also conform to general ecological checkpoints and produce spatial zonation and temporal cycles characteristic of natural systems. The performance of IGBEM is not consistently better than that of BM2, indicating that high levels of physiological detail are not always required when modelling system dynamics. This was reinforced by a section of the study that fitted BM2, IGBEM and an existing ecosystem model (ECOSIM) to Port Phillip Bay. The predictions of all three models lead to the same general conclusions across a range of fishing management strategies and scenarios for environmental change.

Models that are less resolved or use simpler formulations have lower computational demands and can be easier to parameterise and interpret. However, simplification may produce models incapable of reproducing important system dynamics. To address these issues simplified versions of BM2 and IGBEM were compared to the full models to consider the effects of trophic complexity, spatial resolution, sampling frequency and the form of the grazing and mortality terms used in the models on the performance of BM2 and IGBEM. It was clear in each case that some degree of simplification is acceptable, but that using models with very little resolution

or very simplistic linear grazing and mortality terms is misleading, especially when ecosystem conditions change substantially. The research indicates that for many facets of model structure there is a non-linear (humped) relationship between model detail and performance, and that there are some guiding principles to consider during model development. Developmental recommendations include using a sampling frequency of 2 – 4 weeks; including enough spatial resolution to capture the major physical characteristics of the ecosystem being modelled; using quadratic mortality terms to close the top trophic levels explicitly represented in the modelled web; aggregating species to the level of functional groups when constructing the model's trophic web, but if further simplification of the web is necessary then omission of the least important groups is preferable to further aggregation of groups; giving careful consideration to the grazing terms used, as the more complex Holling type responses may be sufficient; and if an important process or linkage is not explicitly represented in the model, or is poorly known, then a robust empirical representation of it should be included.

The work presented here also has implications for wider ecological topics (e.g. the stability-diversity debate) and management issues. Consideration of the effects of trophic complexity on model performance under a range of environmental conditions supports the ecological "insurance hypothesis", but not the existence of a simple relationship between diversity and stability. The biological interactions captured in the web are a crucial determinant of ecosystem and model behaviour, but simple aggregate measures such as diversity, interaction strength and connectance are not. Similarly, the work on the effects of spatial resolution on model performance indicates that spatial heterogeneity is a crucial system characteristic that contributes to many of the emergent properties of the system.

The comparison of the full models with each other, and with ECOSIM, leads to five general conclusions. First, shallow enclosed marine ecosystems react more strongly

to eutrophication than to fishing. Second, a selected set of indicator groups can signal and characterise the major ecosystem impacts of alternative management scenarios and large-scale changes in environmental conditions. Third, policies focusing on the protection of a small sub-set of groups (especially if they are concentrated at the higher trophic levels) can fail to achieve sensible ecosystem objectives and may push systems into states that are far from pristine. Fourth, multispecies and ecosystem models can identify potential impacts of anthropogenic activities and environmental change that a series of single species models cannot. Finally, and most importantly, the use of a single "ultimate" ecosystem model is ill advised, but the comparative and confirmatory use of multiple "minimum-realistic" models is very beneficial.

Acknowledgments

As with any body of work this large there are many, many, people who contributed in some way to its completion (or at least to the survival of the author). There are probably far too many to mention all of them by name, but there are some that deserve special attention.

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Moving into areas less technical, but nonetheless important, I'd like to thank the multitude of people who supported and tolerated me during this period. Thanks to my comrades in arms (Joe, Hugh, Piers, Jeff, Alice, Dirk, Phil and Reg) for the friendship and offers of beer over the last few years (it was all heartily appreciated even if I didn't drink the beer!). A very big thankyou to the Block 3 support crew (Nikki, Bronwyn, Wendy and Tilla) who have been there from the start (when even I wasn't sure what I was doing). An equally huge thank you to the Block 1 crew (David, Helen, Rich, Robin and Sally) who not only leant me their computers, but made sure there was always lots

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Dedication

For my family.

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General Introduction

The question in context

Over the last few decades, and particularly within the last five years, there has been a shift in focus in managing natural resources. For aquatic systems, attention is increasingly moving from specific system components, such as water quality or status of fish stocks, to consideration of entire systems. Unfortunately, many of the tools to facilitate this new focus are still in the early stages of development and understanding. A prime example is ecosystem models. These "whole of system" models first began to appear during the International Biological Program (IBP) in the early 1970s. However, they soon developed a poor reputation (Jørgensen et al. 1992), as many were found not to be cost efficient (Watt 1975) and, more importantly, introducing detail to reflect a growing knowledge base did not necessarily produce good model performance (O'Neill 1975, Silvert 1981, DeCoursey 1992).

With the new focus on system management and substantial increases in computing power, ecosystem models have once again found favour. Unfortunately, the potential pitfalls encountered during the IBP remain. Greater computing power may lift computational constraints, but it cannot solve the issues of uncertainty about model specification and the effects of model structure and detail on model performance (Silvert 1981, Jørgensen 1994). There have been few attempts to systematically consider the effects of model structure on model behaviour and performance, particularly within the realm of marine models. The work presented here attempts to give some insight into the effect of the level of detail in an ecosystem model on the behaviour and performance of the model.

General methodology

Ecological data have a very low signal-to-noise ratio (Silvert 1981). This can

make it difficult to evaluate the effect of model structure on performance if models with modified structure are compared using real data. However, knowledge of the effect of model detail on performance is fundamental to informed model development, interpretation and use. Before a robust understanding of the relationship between model complexity and performance is attained, both data-based and formulation-based issues must be addressed. In approaching these issues, it will be necessary to clearly separate their individual effects.

The research discussed here considers only the effect of model formulation on behaviour and does not attempt to consider effects of data uncertainty. A powerful approach to ascertain the effect of model structure on model behaviour is to use a "deep model-shallow model" comparison. In this approach a simulation model incorporating complex processes, thought to occur in nature, acts as an artificial world or "baseline" against which the performance of other (simpler) models are compared. The simulation model is referred to as a "deep model" and the simpler models that are compared with it are referred to as "shallow models". One of the greatest advantages of this approach is that it allows the modeller to begin with a detailed, but validated, model and then systematically simplify it to determine the level of detail that is sufficient and parsimonious. In addition, it separates those parts of the optimal model complexity issue that are linked to model structure from those dependent only on data, as it deals with perfect knowledge.

The "deep model-shallow model" comparison approach was first used to good effect by Ludwig and Walters (1981, 1985) in fisheries science. The overall approach, of comparing simpler "assessment" models against more complex ones, has since become a useful means of evaluating fishery harvest strategies, including stock assessment methods, for single species fisheries management. In this context the approach has been referred to as "operational management procedures" (Butterworth

and Punt, 1999) or "management strategy evaluation" (Smith et al. 1999). More recently it has been extended to cover evaluations containing multi-species interactions (Sainsbury et al. 2000, Punt et al. in press).

Biogeochemical ecosystem models were chosen as the basis for this study because they capture processes known to be physically and biologically important determinants of ecosystem behaviour. They also represent some of the most complex ecosystem models available and so there is a lot of scope for simplification and consideration of the effects of many aspects of model structure on performance. Biogeochemical ecosystem models explicitly include complex trophic webs, nutrient dynamics and recycling, temporal variation and forcing. They can also be spatially resolved and include highly detailed process formulations. The degree of detail employed in the formulation of any one of these features may have an impact upon model behaviour and performance. Moreover, nutrient loading and fishing are two of the biggest anthropogenic forces on coastal marine systems, and as biogeochemical ecosystem models explicitly employ nutrients and a trophic structure spanning primary producers to fish, it was possible to consider the robustness of any results to the effects of changing anthropogenic forcing of the system. There are other successful types of ecosystem model that use alternative assumptions and formulations. For example, ECOSIM (Walters et al. 1997) is a dynamic simulation model that assumes mass balance and explicitly incorporates top-down *vs.* bottom-up control, but it does not include nutrient dynamics (using biomasses only), is not explicitly spatially structured (assumes homogeneous spatial behaviour) and does not usually incorporate temporal forcing. While knowledge of the sensitivity of ECOSIM to facets of its structure such as the trophic complexity is necessary (Walters pers. com.), in comparison with biogeochemical models, ECOSIM and other types of ecosystem model do not readily allow consideration of the same range of complexity issues and forcing conditions.

However, comparison of biogeochemical ecosystem models with these other types of ecosystem model is a good way of checking for the effects of underlying system and model assumptions on model behaviour.

This thesis

The first chapter introduces the "deep" ecosystem model, referred to as the Integrated Generic Bay Ecosystem Model (IGBEM). This model is the most detailed model used in the study and is one of two principle "deep" models in the "deep-shallow model" comparison. Its formulation and development is presented, as is an analysis of its performance assessed against real marine systems from around the world. This analysis indicates that the model reproduces realistic dynamics and levels of biomass and therefore provides a sound basis for the study of model complexity and structure.

In chapter 2 I introduce the second total ecosystem model developed in the study, Bay Model 2 (BM2). This model has a two-fold purpose. First, because it is simpler in formulation than IGBEM, it provides a form of "shallow" model. Second, it is sufficiently detailed to also act as a "deep model" when considering the effects of model structure on behaviour by reducing detail or scope. The development and validation of the model as a generic system is presented, and the effect of reducing physiological detail on model behaviour relative to IGBEM is examined. The question of whether BM2 performs as well as IGBEM is crucial because although physiologically intensive ecosystem models are used (Baretta et al. 1995, Baretta-Bekker and Baretta 1997) they are controversial because they have large data and maintenance requirements (Murray and Parslow 1999b). If simpler formulations perform as well as physiologically intensive ones then this will temper some of the controversy surrounding complex ecosystem models.

While chapter 2 considers performance of BM2 in the context of temperate

marine bays in general, in chapter 3 I extend the analysis presented in chapter 2 to consider two specific bays (Port Phillip Bay in Australia and Chesapeake Bay in the USA). This analysis of the effect of process detail on model behaviour considers the models' abilities in specific circumstances. Generic models are good for developing theory and general understanding, but models are usually applied to specific locations and there can be system specific concerns about model behaviour. Thus, consideration of the effects of model complexity on performance in specific systems is necessary.

The fourth chapter is concerned with specific aspects of the implementation of IGBEM and BM2, and treats both models as "deep models". I address the effect of spatial resolution and sampling frequency (the temporal spacing of output) on model behaviour and how accurately it is interpreted. These are important issues that have been central concerns in ecology and ecological modelling for over 40 years (Huffaker 1958, MacArthur and Wilson 1967, Levins 1970, Levin 1992, Keitt 1997, Rantajärvi et al. 1998). The sampling scale (spatial and temporal) used in field studies and in models has logistical implications (the more intensive the sampling the more it costs to collect, store and analyse). It can also potentially affect the processes observed in the field and how they are interpreted (Roughgarden et al. 1988, Rantajärvi et al. 1998), and in models it can impact on both model predictions (Murray 2001) and the stability of the modelled system (Gurney and Nisbet 1978, Hassell et al. 1994, Sharov 1996, Keitt 1997).

The fifth chapter examines the effect of trophic complexity on the performance of IGBEM and BM2. It addresses how much of the web is needed to capture the important dynamics, and the sensitivity of model performance to the way in which the web is constructed. This is another issue that has occupied ecology and ecological modelling for decades. In ecology, the debate over the relationship between stability and diversity in foodwebs has focused on trying to determine which webs are stable and

why (Odum 1953, MacArthur 1955, May 1973, Pimm and Lawton 1978, Yodzis 1981, Harding 1999, Yachi and Loreau, 1999, McCann 2000). However, as construction of simpler models is often a goal (Iwasa et al. 1987, Sugihara et al. 1984, Lee and Fishwick 1998), simplifying trophic complexity in models has received some attention (Zeigler 1976, O'Neill and Rust 1979, Cale et al. 1983, Iwasa et al. 1987, Yodzis 2000). There are two main ways in which trophic webs can be simplified, either by omitting trophic groups or by aggregating several similar groups into a single component. Both of these methods are commonly used in developing ecosystem models, but in the past the effects of these decisions on model performance have not received equal attention as researchers have largely concentrated on the effects of aggregating groups. Therefore, here I consider their relative affects on model performance.

Chapter six considers two other specific aspects of model structure and its impact on the dynamics of the BM2 model. I evaluate the form of the grazing term (or functional response) used in the model and the way in which the model is 'closed' (the form of the mortality terms imposed on the highest groups in the modelled web). Both aspects are recognised as potentially having considerable effects on the dynamics of multispecies models (May 1976, Hassell and Commins 1978, Begon and Mortimer 1986, Steele and Henderson 1992, Edwards and Brindley 1999, Murray and Parslow 1999a, Tett and Wilson 2000, Gao et al. 2000), but their effect on ecosystem models has received little attention.

In chapter 7 I compare biogeochemical models, IGBEM and BM2, with another ecosystem model, ECOPATH with ECOSIM. In this case all the models are calibrated to Port Phillip Bay. The objectives of this part of the study are to compare the predictions of the models under changing conditions (nutrient loads and fishing rates) or alternative management policies, and to ascertain whether there are commonalities and general conclusions that are robust to model structure and formulation. This comparison

also served to examine the effect of structure on model behaviour, as the three models are dissimilar in their data requirements, underlying assumptions, trophic complexity and process detail. A comparative and confirmatory approach to the consideration of the potential effects of management policies and changes in ecosystem conditions, such as the one in this chapter, is one of the most effective ways of using ecosystem models (Reichert and Omlin 1997, Steele 1998, Duplisea 2000, Yodzis 2001a and b).

The final chapter reviews the topic of model structure and performance by synthesising the findings of the present study in the context of published work on the topic. While some clear guidelines emerge, it is clear that the field is still in an early stage of development and much remains to be done.

Chapter 1 An Integrated Generic Model of Marine Bay Ecosystems

Abstract

The Integrated Generic Bay Ecosystem Model (IGBEM) is presented. It is a coupled physical transport-biogeochemical process model constructed as a basis to explore the effects of model structure and complexity. The foundations for the model are two existing models, the European Regional Seas Ecosystem Model II (ERSEM II) and the Port Phillip Bay Integrated Model (PPBIM). Additional components (such as benthic herbivorous invertebrates) and certain sub-models (to do with sediment chemistry and mixing) had to be incorporated or modified to allow for extra factors of interest and a seamless amalgam of ERSEM II and PPBIM. The standard form of the entire model compares well with real systems, with similar physical features and of varying eutrophication schemes, from Chesapeake Bay through to Port Phillip Bay Australia. Furthermore, IGBEM conforms to general ecological checkpoints and produces spatial zonation and long term cycles characteristic of natural systems. Despite the model taking a generalised biomass per functional group form it captures crucial system resource dynamics well and allows for some exploration of the effects of ecological driving forces such as predation and competition.

Keywords

biogeochemical, model, ecosystem, ERSEM, Port Phillip Bay

1.1 Introduction: marine ecosystem models

There has been a proliferation of marine ecosystem models within the last two decades with literally hundreds, of varying scope and quality, in existence. Most are mass balance models, of Eulerian formulation, which typically concentrate on either end of the trophic chain, i.e. fish or nutrients and phytoplankton, but rarely both. Those that

couple physics and biology tend to do so by linking sub-models that approach the respective processes in quite different ways. Physical attributes are often dealt with via a number of common and well defined methods, including box models, specified (often Lagrangian) flows, prognostic dynamical flow models or general circulation models. The most common methodologies employed in the biological side of ecosystem models are pooled models (which conserve some biogeochemical currency within a chain, or small network, of compartments that represent functional groups or trophic levels), multispecies formulations (allowing for more realistic webs) and structured population models. Generally speaking, it emerges that box models and specified flows are the best way of considering biological processes in realistic flow environments, free of the complexity of directly calculating the flow itself. It is also apparent that pool models provide a useful framework for constructing a variety of models (Olson and Hood 1994). Models such as the European Regional Seas Ecosystem Model (ERSEM) (Baretta et al. 1995) mix and match biological formulations based on trophic identity to capture the critical performance of the different components.

The felicitous history of reductionist physical models was probably one of the driving forces behind the bloom of highly detailed deterministic ecosystem models during the 1970s (Young et al. 1996). However, it became apparent that complicated models did not necessarily capture system dynamics well and there was a wide spread and rapid return to simpler or more circumscribed models. With the advent of more powerful computers and the push for an ecosystem perspective for resource and environmental management, detailed ecosystem models are again finding some measure of favour. While there is still debate about their usefulness for management, given their dependence on exceedingly large numbers of, often uncertain, parameter values, they are useful for locating gaps in our current understanding as well as learning about system behaviour and its determinants. It is in this context that the Integrated Generic

Bay Ecosystem Model (IGBEM) was constructed. Consequently, it is not intended as a simulated replica of any one system. For convenience it does utilise the physics of a particular Australian bay (Port Phillip Bay, Melbourne (Figure 1.1)), but it has the general biology and functional groups typical of most temperate bays.

IGBEM was constructed as a first step in understanding the effects of model structure and complexity on model behaviour and thereby deriving some guidelines to optimal model complexity. Though not a strict requirement, it was thought that such an exercise would benefit from being built upon a reference model that resembled reality as much as possible. Here we outline construction of the model and explore its capacity to reflect real world behaviours.

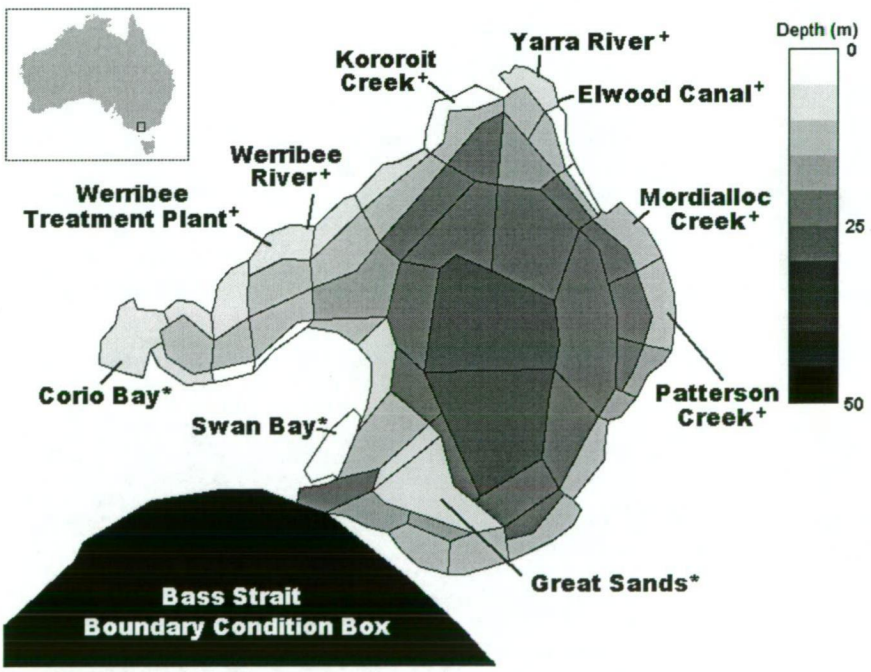


Figure 1.1: Map of box geometry used for the standard runs of the Integrated Generic Bay Ecosystem Model. It represents Port Phillip Bay, Melbourne, Australia (location marked on map inset). Important geographical features (marked with *) and point source-sinks used in the model (marked by +) are indicated.

1.2 Building IGBEM

Port Phillip Bay (PPB) has a number of features that make it an attractive site for learning. It is a large marine embayment, approximately 1930 km^2, that has over half its volume in waters less than 8 m (it is 24m at its deepest point). Only 8 drainage basins directly run off into the bay. Extensive sandbars form a tide delta in the southern end of the bay and these restrict exchange between the bay and the open waters of Bass Strait. This physically contained environment is therefore free of many of the often-worrisome issues that are associated with boundary conditions. Since approximately three million people reside within the urbanised portions of the bay's catchment area, the bay is also under some of the stresses faced by other major temperate bays. Accordingly it is a prime site to study ecosystem dynamics, human impacts and how they might best be modelled. Fortuitously it has also been the subject of intensive study over many years, which provides an extensive knowledge base to build from.

The biogeochemical model created as part of the most recent PPB study is both detailed and successful (Murray and Parslow 1999a). However, as it is based on the biogeochemistry of only the lower trophic levels it is not a suitable vehicle for the examination of the effects of ecosystem model complexity and formulation, when considering fisheries and eutrophication simultaneously. Since the Port Phillip Bay Integrated Model (PPBIM) by Murray and Parslow (1999a) does not cover enough faunal groups, it was necessary to use another model to extend PPBIM to produce a suitable generic model. The European Regional Seas Ecosystem Model II (ERSEM II) (Baretta et al. 1995, Baretta-Bekker and Baretta 1997) is well suited to being grafted to PPBIM, as it is a marine biogeochemical boxmodel with a similar architecture and it includes more process detail than PPBIM and additional faunal groups. Between them, PPBIM and ERSEM II include most of the major groups and processes thought to be important in coastal marine systems and they represent state-of-the-art biogeochemical

models.

IGBEM was created by tying together the biological and physical sub-models of PPBIM (Murray and Parslow 1997 and 1999a) and the biological modules from ERSEM II (Baretta et al. 1995, Baretta-Bekker and Baretta 1997). The 4 submodels of PPBIM, 3 biological ones (water column, epibenthic, sediment) and a physical submodel, formed the framework for IGBEM and the various ERSEM II modules were translated and added directly to the appropriate sub-model. For those functional groups that are covered by both ERSEM II and PPBIM both formulations are included in IGBEM with a switch setting determining which is in use in any one run. Only the ERSEM II formulations were employed in the runs presented here.

The final form of IGBEM provides a spatially and temporally resolved model of nutrient cycles in an enclosed temperate bay. The model has twenty-four living components, two dead, five nutrient, six physical and two gaseous components (Table 1.1). These components are linked through both biological and physical interactions and the resultant network (Figure 1.2) is reminiscent of flow diagrams for real systems. The model is replicated spatially using the 3 layer (water column, epibenthic, sediment), 59-box geometry developed for PPBIM. Thus, the set of polygons and their bathymetry map a physical area that represents PPB (Figure 1.1). Temporally, a daily time-step is utilised for the standard runs of IGBEM as this best matches the transport model which underlies the physical sub-model of IGBEM, and is little different from that of PPBIM. The use of the transport model means that, like PPBIM, IGBEM is driven by seasonal variations in solar irradiance and temperature, as well as nutrient inputs from point sources, atmospheric deposition of dissolved inorganic nitrogen (DIN) and exchanges with the Bass Strait boundary box. Further details of the transport model, the rationale behind its use and how it links into the biological submodels of PPBIM can be found in Walker (1999) and Murray and Parslow (1999a). The level of process detail used in the

IGBEM formulations and IGBEM's diet matrix are outlined in Tables 1.2 and 1.3 respectively.

Table 1.1: List of components in the Integrated Generic Bay Ecosystem Model (IGBEM) compared to those in the Port Phillip Bay Integrated Model (PPBIM) and the biological modules of the European Regional Seas Ecosystem Model II (ERSEM II). All living and dead components have C, N and P pools.

		Model		
Component	**Codename**	IGBEM	ERSEM II	PPBIM
Diatoms*	PL	Y	Y	Y
Autotrophic flagellates	AF	Y	Y	
Picophytoplankton	PS	Y	Y	Y
Dinoflagellates	DF	Y	Y	Y
Pelagic bacteria	PB	Y	Y	
Heterotrophic flagellates	HF	Y	Y	
Microzooplankton	ZS	Y	Y	Y
Large omnivorous zooplankton	ZL	Y	Y	
Large carnivorous zooplankton	ZLC	Y	Y	Y
Planktivorous fish	FP	Y	Y	
Piscivorous fish	FV	Y	Y	
Demersal fish	FD	Y	Y	
Demersal herbivorous fish	FG	Y		
Macroalgae	MA	Y		Y
Seagrass	SG	Y		Y
Microphytobenthos*	MB	Y		Y
Macrozoobenthos (epifaunal carnivores)	MZ	Y	Y	
Benthic (epifaunal) grazers	BG	Y		
Benthic suspension feeders	BF	Y	Y	Y
Infaunal carnivores	BC	Y	Y	
Benthic deposit feeders	BD	Y	Y	
Meiobenthos	OB	Y	Y	
Aerobic bacteria	AEB	Y	Y	
Anaerobic bacteria	ANB	Y	Y	
Labile detritus	DL	Y	Y	Y
Refractory detritus*	DR	Y	Y	Y
DON	DON	Y	Y	Y
DIP	DIP	Y	Y	Y**
Ammonia	NH	Y	Y	Y
Nitrate	NO	Y	Y	Y
Dissolved silicate	Si	Y	Y	Y
Dissolved oxygen	O2	Y	Y	Y**
Carbon dioxide	CO2	Y	Y	
Light	IRR	Y	Y	Y
Salinity	SAL	Y		Y
Sediment grain types	PHI	Y		Y
Bottom stress	STRESS	Y		Y
Porosity	PORE	Y		Y
Volume	VOL	Y		Y

* Also have an Si internal pool.

** Handled as nitrogen fluxes scaled by the Redfield ratio N:C:P:O:Si = 1:5.7:0.143:16:3 (from Murray and Parslow 1997)

Figure 1.2: Biological and physical interactions between the components used in the Integrated Generic Bay Ecosystem Model IGBEM). A '*' indicates those components from the Port Phillip Bay Integrated Model, and those in **bold** are components built specifically for IGBEM, while the remainder are from the European Regional Seas Ecosystem Model II (Blackford and Radford 1995). The code for each component is given by its name.

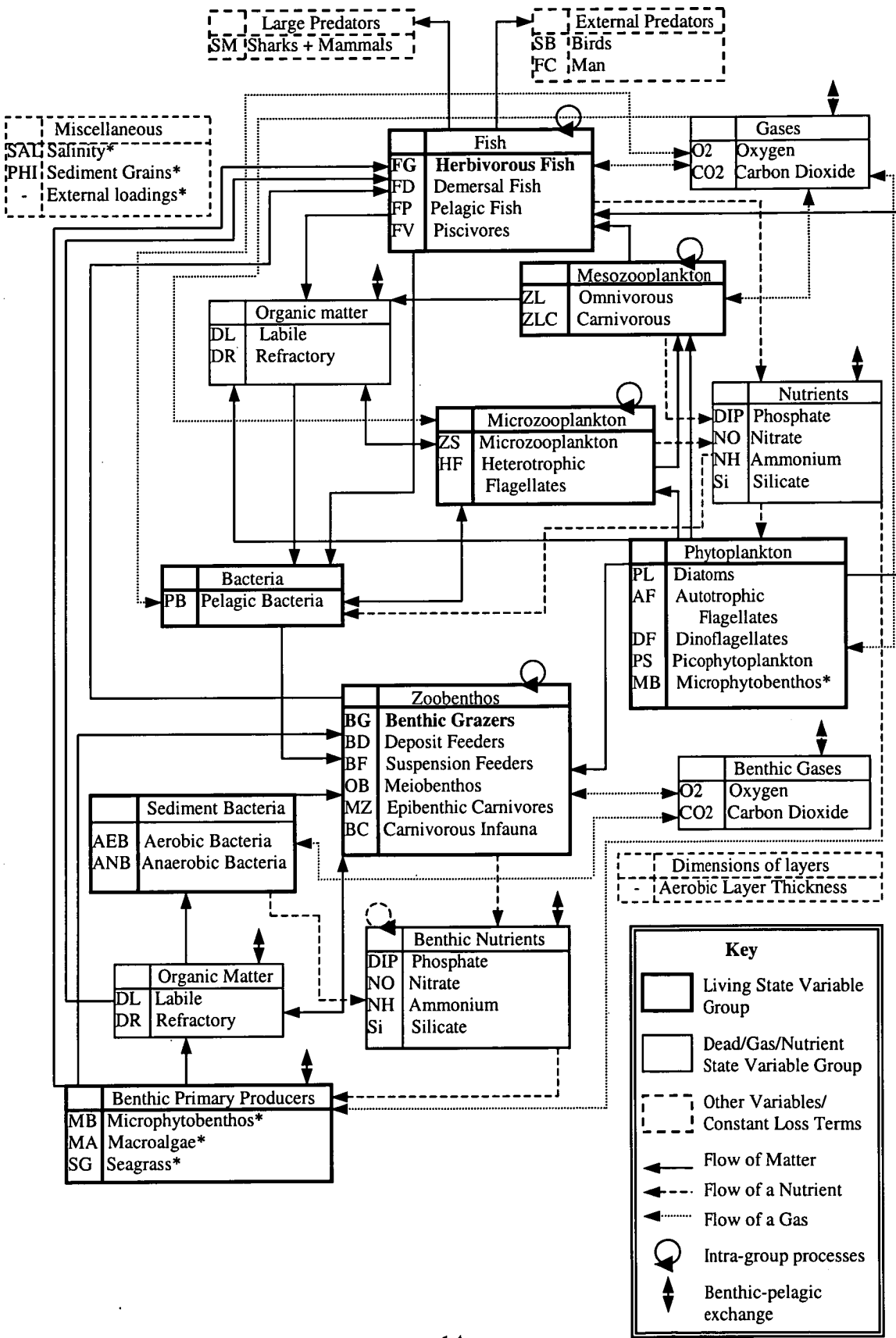


Table 1.2: Level of detail used in the model formulation for each of the processes carried out in a standard run of the Integrated Generic Bay Ecosystem Model. Component codes are as stated in Table 1.1 (except for C, N, P, Si which are Carbon, Nitrogen, Phosphorous and Silica respectively). The symbols indicate the formulation used for each process as follows: **a**ctivity; **b**asal; **c**onstant (not dynamic); **d**ynamic; DIN (**e**piphytic growth) effect; search and **h**andling times included; **i**nternal pool controls; **l**ight limitation; depth effect (**m**); **n**utrient effect; **o**xygen effect; **p**erforms this physical activity; **r**est; **s**tarvation; **t**emperature effect; **c**rowding; assumed in formulation but not explicit; **p**hysical bottom stress effect; present (+); absent (-). ** indicates that there is a flux of C from the static returns, but in the form of carbon dioxide.

Process	Component																	
Water Column	C	N	P	Si	PL	DF	AF	PS	PB	ZS	HF	ZL	ZLC	FP	FV	MB	DR	DL
Used by phytoplankton	+	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Used by bacteria	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+
Flux from excretion	+	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-	+	+
Mineralisation	-	-	-	-	-	-	-	-	p	-	-	-	-	-	-	-	+	+
Nitrification	-	+	-	-	-	-	-	-	p	-	-	-	-	-	-	-	-	-
Oxygen production	-	-	-	-	+	+	+	+	-	-	-	-	-	-	-	+	-	-
Growth	-	-	-	-	lnt	lnt	lnt	lnt	ra	+	+	+	+	+	+	lnt	-	-
Respiration	-	-	-	-	ra	ra	ra	ra	o	ra	ra	ra	ra	ra	ra	ra	-	-
Lysis (nutrient stress)	-	-	-	-	+	+	+	+	-	-	-	-	-	-	-	+	-	-
Nutrient uptake	-	-	-	-	i	i	i	i	-	-	-	-	-	-	-	i	-	-
Predation losses	-	-	-	-	+	+	+	+	+	+	+	+	+	cd	cd	+	+	+
Cannibalism	-	-	-	-	-	-	-	-	-	+	+	+	+	-	+	-	-	-
Grazing (consumption)	-	-	-	-	-	-	-	-	-	+	+	h	h	h	h	-	-	-
Natural mortality	-	-	-	-	x	x	x	x	+	o	o	o	o	bs	bs	x	-	-
Excretion	-	-	-	-	i	i	i	i	i	i	i	i	i	i	i	i	-	-
Faeces	-	-	-	-	-	-	-	-	+	+	+	+	+	+	+	-	-	-
Flux from static returns[1]	**	+	+	-	-	-	-	-	+	-	-	-	-	-	-	-	+	+
Sediment	C	N	P	Si	BD	BC	OB	AEB	ANB	PL	DF	PS	AF	MB	DR	DL		
Used by microphytobenthos	+	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-		

Process	Component															
	C	N	P	Si	BD	BC	OB	AEB	ANB	PL	DF	PS	AF	MB	DR	DL
Used by bacteria	+	+	+	-	-	-	-	-	-	-	-	-	-	-	ontm	ontm
Flux from excretion	+	+	+	+	-	-	-	-	-	-	-	-	-	-	+	+
Mineralisation	-	-	-	-	-	-	-	p	p	-	-	-	-	-	+	+
Nitrification	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Denitrification	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Oxygen production[2]	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-
Growth	-	-	-	-	ot	ot	ot	ra	ra	-	-	-	-	lnt[2]	-	-
Respiration	-	-	-	-	ra	ra	ra	otra[2]	otra[2]	-	-	-	-	ra	-	-
Nutrient uptake	-	-	-	-	-	-	-	ontm	ontm	-	-	-	-	i	-	-
Predation losses	-	-	-	-	+	+	+	+	+	-	-	-	-	+	+	+
Cannibalism	-	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-
Grazing (consumption)	-	-	-	-	+	+	+	-	-	-	-	-	-	-	-	-
Natural mortality	-	-	-	-	ot	ot	ot	+	+	+	+	+	+	+	-	-
Excretion	-	-	-	-	i	i	i	i	i	-	-	-	-	i	-	-
Faeces	-	-	-	-	+	+	+	-	-	-	-	-	-	-	-	-
Impact upon bioirrigation/bioturbation	-	-	-	-	+	+	+	-	-	-	-	-	-	-	-	-

Epibenthic	C	N	P	Si	MZ	BF	BG	MA	SG	FD	FG	DR	DL
Used by macrophytes	+	+	+	-	-	-	-	-	-	-	-	-	-
Flux from excretion	-	-	-	-	-	-	-	-	-	-	-	+	+
Oxygen production	+	+	+	-	-	-	-	-	-	-	-	+	+
Growth	-	-	-	-	-	-	-	+	+	-	-	-	-
Respiration	-	-	-	-	ot	ot	ot	lntw	lntw	+	+	-	-
Lysis (nutrient stress)	-	-	-	-	ra	ra	ra	x	x	ra	ra	-	-
Nutrient uptake	-	-	-	-	-	-	-	+	+	-	-	-	-
Predation losses	-	-	-	-	+	+	+	+	+	cd	cd	+	+
Cannibalism	-	-	-	-	+	-	-	-	-	+	-	-	-
Grazing (consumption)	-	-	-	-	+	+	+	-	-	h	h	-	-
Natural mortality	-	-	-	-	ot	ot	ot	by	be	bs	bs	-	-
Excretion	-	-	-	-	i	i	i	an	an	i	i	-	-
Faeces	-	-	-	-	+	+	+	-	-	+	+	-	-
Flux from static returns[1]	-	-	-	-	-	-	-	-	-	-	-	+	+
Impact upon bioirrigation and bioturbation	-	-	-	-	+	+	+	-	-	-	-	-	-

1. i.e. a % of the losses to fishing/seabirds/large predators
2. used to determine the oxygen horizon

Table 1.3: Diet matrix for the living components in a standard run of the Integrated Generic Bay Ecosystem Model. Component codes are as for Table 1.1. A "+" indicates a feeding link, "-" no link and a "0" is a potential link (implemented but the availability-preference parameter for that prey item is set to zero in the standard runs.)

	Grazer															
Prey	ZS	HF	ZL	ZLC	FP	FV	FD	FG	AEB	ANB	OB	BD	BC	BF	MZ	BG
PL	+	-	+	-	+	-	-	-	-	-	-	-	-	+	-	-
PS	+	+	0	-	-	-	-	-	-	-	-	-	-	+	-	-
AF	+	+	+	-	-	-	-	-	-	-	-	-	-	+	-	-
DF	-	-	0	-	-	-	-	-	-	-	-	-	-	-	-	-
ZS	+		+	+	-	-	-	-	-	-	-	-	-	-	-	-
HF	+	+	+	0	-	-	-	-	-	-	-	-	-	-	-	-
ZL	-	-	+	+	+	+	-	-	-	-	-	-	-	-	-	-
ZLC	-	-	+	+	+	+	-	-	-	-	-	-	-	-	-	-
FP	-	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-
FV	-	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-
FD	-	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-
FG	-	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-
PB	0	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-
AEB	-	-	-	-	-	-	-	-	-	-	+	+	-	+	-	-
ANB	-	-	-	-	-	-	-	-	-	-	+	+	-	-	-	-
OB	-	-	-	-	-	-	-	-	-	-	+	+	+	-	-	-
BD	-	-	-	-	-	-	+	-	-	-	-	-	+	-	+	-
BC	-	-	-	-	-	-	+	-	-	-	-	-	+	-	+	-
BF	-	-	-	-	-	-	+	-	-	-	-	-	-	-	+	-
MZ	-	-	-	-	-	-	+	-	-	-	-	-	-	-	+	-
BG	-	-	-	-	-	-	+	-	-	-	-	-	-	-	+	-
MB	+	-	0	-	-	-	-	+	-	-	+	+	-	+	-	-
MA	-	-	-	-	-	-	0	+	-	-	-	-	-	-	+	+
SG	-	-	-	-	-	-	0	+	-	-	-	-	-	-	+	+
DR	0	0	0	0	-	-	-	-	+	+	+	+	-	-	-	-
DL	-	-	-	-	-	-	-	+	+	+	+	+	-	+	-	+

Some components and processes in IGBEM do not feature in PPBIM or ERSEM II, or have been modified from their original formulation to enable synthesis of the two models. Important additions are components for epibenthic herbivorous scavengers and herbivorous fish. These were added to take advantage of the macrophyte food sources represented in PPBIM. These components were written by duplicating the general form of appropriate existing components (using ERSEM's 'standard organism' concept (Baretta et al. 1995)) and then adjusting diets and parameter values to those representative of herbivorous grazers. Consumption of these new groups by predatory groups within the model was also added (see the diet matrix, Table 1.3) based on diet data from the literature (Shepherd and Thomas 1982, Heymans and Baird 1995, Levinton 1995, Kuiter 1996, Gunthorpe et al. 1997).

Two biological components were modified in integrating PPBIM and ERSEM II. Microphytobenthos was included with minor modification after Blackford (1999). Also, the benthic suspension feeders of ERSEM II had their diets and habits modified slightly to better match those of PPBIM. This involved changing one of their dietary components from refractory to labile detritus and including an incidental transfer of refractory detritus from the water column to the sediment via suspension feeding.

A number of the original chemical and physical processes in PPBIM and ERSEM II required modification. The highly refractory detritus of ERSEM II, which has a very slow breakdown rate (on the order of a century or more) was omitted. The component referred to as refractory detritus in IGBEM is the equivalent of ERSEM II's "Slowly degradable organics". The formulation of bioirrigation implemented in PPBIM was left intact for IGBEM, but it is tied to the dynamical sediment fauna via an "enhancement" term similar to that of ERSEM I (Ebenhöh et al. 1995). In contrast, bioturbation received more attention in IGBEM than in PPBIM. Bioturbation was considered during the formulation of PPBIM, but it was never implemented (Walker

1997), whereas it is a working part of ERSEM I (Ebenhöh et al. 1995). The inclusion of well-elaborated formulations of bioturbation (a good example being that of Francois et al. 1997) in an ecosystem model is no more feasible now then when ERSEM I was originally formulated (Ebenhöh et al. 1995), so simple approximations are necessary. IGBEM uses explicit sediment layers and includes the sediment mixing processes of particulate diffusion, expulsion (whereby material at depth is moved to the surface), and exchange (where material at the surface and at depth are exchanged). The only components (tracers) acted upon by bioturbation were those particulate tracers that were allowed in the sediments and were not macrobenthos. That is, sediment grains, settled phytoplankton, microphytobenthos, meiobenthos, detritus and sediment bacteria. The approximation used in IGBEM represents particulate diffusion, expulsion and exchange with the surface by transferring sediment between the appropriate layers of the model. Accordingly, the formulation implemented expresses the tracer concentration in the *i*th sediment layer (Ci(t)) at the end of a time step as:

$$C_i(t+\Delta t)=\frac{C_{i+1}(t)\cdot k_{i+1}+C_{i-1}(t)\cdot k_{i-1}+C_i(t)\cdot z_i-2C_i(t)\cdot k_i-C_i(t)\cdot m_i-C_i(t)\cdot g_i+C_0(t)\cdot g_0}{k_{i+1}+k_{i-1}+z_i-2k_i-m_i-g_i+g_0} \quad (1.1)$$

$$k_i=\frac{\psi\cdot\delta\cdot\tau\cdot\theta_i}{z_i} \quad (1.2)$$

$$m_i=\gamma\cdot\delta\cdot\tau\cdot\theta_i \quad (1.3)$$

$$g_i=\eta\cdot\delta\cdot\tau\cdot\theta_i \quad (1.4)$$

Where k_i represents the thickness transferred from i due to particulate diffusion, m_i is the thickness moved to the surface from layer *i* by expulsion and g_i is the thickness moved from layer *i* due to exchange with surface layers and z_i is the thickness of layer *i*. The thicknesses k_i, m_i and g_i only differ in a single parameter. For the parameters they share, δ represents the base density of biological activity; τ represents the modification to the baseline to reflect dynamic sediment fauna activity in the ecological sub-model

(calculated in much the same way as that of ERSEM (see Ebenhöh et al. 1995)); and θ_i is the depth dependence of the mixing process (this is a simple functional form, as of PPBIM, and though usually constant it is also possible to implement linear, parabolic and half-Gaussian forms (Walker 1997)). The parameter which does differ in the calculation of k_i, m_i and g_i is the base rate of each process - ψ is the rate of particle diffusion (m^2 per Δt per unit biomass of bioturbative benthos per m^2), γ is the rate of expulsion (m per Δt per unit biomass of bioturbative benthos per m^2) and η is the rate of exchange between the surface and deeper layers (m per Δt per unit biomass of bioturbative benthos per m^2). These simple representations minimise computational costs and perform satisfactorily for the amounts involved under the model geometry used in standard runs. A small amount of burial of sediments and associated detrital particles is also enabled in IGBEM.

The implementation of sediment chemistry in IGBEM also differed from that of ERSEM II and PPBIM. An attempt was made to make the empirical model of PPBIM (Murray and Parslow 1999a) more dynamic by incorporating more of the processes included in the calculation of ERSEM I's density profiles. This highlighted the crucial importance of the denitrification submodel. Blackford (1997) noted that ERSEM II underestimated the levels of bacterial biomass in the sediments and this was also very true of IGBEM. As a consequence any attempt to use bacterial activity to set levels of nitrification and denitrification failed and the model output took on a "eutrophied" form regardless of the levels of nutrient loading. In the short term this problem was solved by reverting to using Murray and Parslow's (1999a) sediment chemistry model and retaining bacteria only as tracers (as they had inherent value as indicators of system state). All the runs presented here were completed in this way. In the long term a new way of considering bacteria was developed as part of a related ecosystem model (chapter 2).

Space precludes detailing the many other alternative settings that were built into the model. These alternatives included forage- and density-dependent movement of fish (in place of the prescribed movement of ERSEM II), invasions by specific functional groups, fishing induced mortality on non-target groups and a basic effort model for the fishery. Alternatives that were used in runs discussed here are identified below.

The parameter set used for IGBEM is based on the combined parameter sets of PPBIM and ERSEM II (corrected so that everything is at a reference temperature of 15 degrees Celsius and in mg m^{-3} (or mg m^{-2} if epibenthic)). Calibration of the model was required to ensure mass balance and to achieve stability. However, the large number of parameters (in excess of 775, disregarding those duplicated spatially or with age) means that a systematic sensitivity analysis is not possible. Thus, growth and mortality parameters and those associated with processes producing the greatest divergences or instability were calibrated until stability was achieved and all functional groups persisted. The restriction imposed on this calibration is that final parameter values must be within the range of values recorded in the available literature for that parameter.

1.3 Model runs

All functional groups are active in the standard run of IGBEM. Runs usually simulate a 20 year period, but a few simulate 100 years to allow consideration of long term cycles and to check whether the model has reached a representative state by the end of the usual 20 year run. The files containing the forcing for the transport model cover only 4 years and so are looped such that when the model reaches the end of a 4-year period it returns to the start of the forcing files and repeats them.

The standard run of IGBEM has fish migration as a forcing function, like ERSEM II (Bryant et al. 1995) and fish recruitment is identical in time and space from year to year, though the exact date of recruitment can vary by a few weeks. To check

the impact of these assumptions an alternative movement scheme and a number of alternative recruitment schemes were also tried. The alternative form of fish migration is forage- and density-dependent and fish are distributed among spatial cells based on available food resources in relation to metabolic requirements. The alternative recruitment formulations include a Beverton-Holt stock recruitment curve; a case where recruitment is related to primary production (used as a proxy for larval resource availability); and a random number drawn from a lognormal distribution, which simulates the often observed pattern of recruitment where there is the occasional very strong year class. Each of these alternative forms was parameterised such that the mean number of recruits returned would be very similar in each case and also very close to that given by the constant case in the initial state of the system (Table 1.4).

Table 1.4: Alternative regimes for fish recruitment implemented in the Integrated Generic Bay Ecosystem Model. Note b_{tj} is the number of recruits added to box j at time t.

Recruitment Regime	Formulation	Definition of Specific Terms
Standard	$b_{tj} = J_t$	J_t = element t of the recruitment vector (constant spatially and temporally)
Beverton-Holt stock-recruit relationship (distributed evenly across the recruitment period)	$b_{tj} = \frac{\left(\frac{\alpha \cdot L_{tj}}{\beta + L_{tj}}\right)}{t_x}$	α = Beverton-Holt α for the fish group β = Beverton-Holt β for the fish group L_{tj} = biomass of larvae in box j at time t t_x = total length of recruit period
Proportional to Primary Production	$b_{tj} = \frac{\eta_{FX} \cdot CHL_{j,t}}{\eta_{chl}}$	η_{FX} = recruitment coefficient for fish group FX $CHL_{j,t}$ = water column chlorophyll in box j at time t η_{chl} = reference level of chlorophyll (1.5)
Lognormal distribution	$b_{tj} = \frac{\lambda_{FX}}{y \cdot \sigma \cdot \sqrt{2 \cdot \pi}} e^{\left(\frac{-(\log y - \mu)^2}{2 \cdot \sigma^2}\right)}$	λ_{FX} = recruitment multiplier for fish group FX $y \sim U(0,1)$ $\sigma = 0.3$ $\mu = -0.5$ $\pi = 3.141592654$

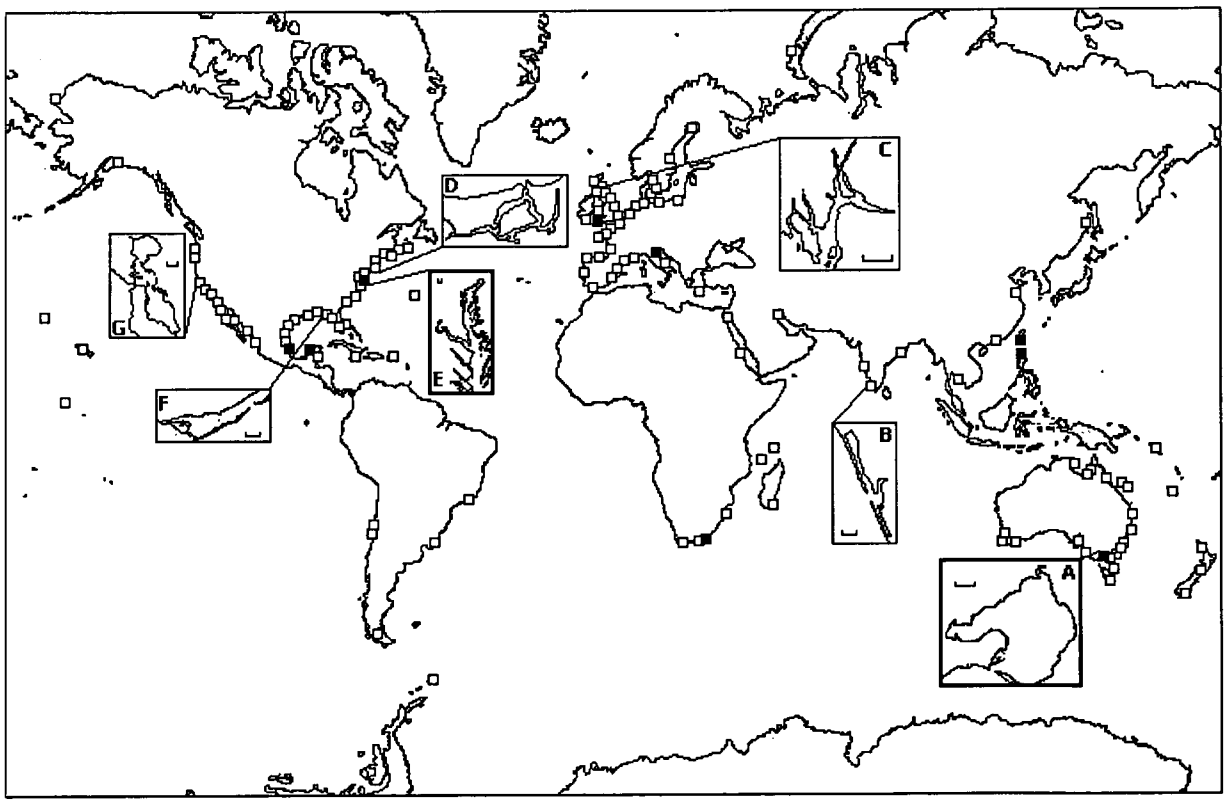
To evaluate how well the model replicates existing systems a number of other bays around the world that have similar physical conditions (tidal range and relative size of opening to the sea) (Figure 1.3) were identified. The inputs to these bays (from Monbet 1992) were then scaled based on the area of the bay relative to PPB and then the nutrient forcing files for IGBEM were adjusted to match. Thus, while the exact geography of the bay was not changed, nutrient conditions were altered to try and capture the state of several well-studied bays. Only minimal changes were made to the biological parameters of the system. Since the biological parameters for the run under baseline conditions have not been tuned to the species composition of any particular bay to begin with, but are based on species from temperate marine bays in many parts of the world, the decision not to tune the biological parameters in each case is justified. The ability to achieve a plausible representation of these other bays was based on the model's output values for chlorophyll a (chl a), DIN, biomasses and other measures identified from the literature.

1.4 Results and discussion

1.4.A IGBEM vs real bays

Information on each of the individual components present in the model is not generally available for real bays. Consequently output has to be pooled so that it matches the most common resolution of the data available in the literature. To differentiate between the individual functional groups of IGBEM and the pooled forms of the output, the latter are referred to as trophic sets. The list of trophic sets is made up of chl a (as a proxy for total phytoplankton), zooplankton, fish, macrophytes, microphytobenthos, meiobenthos, benthos (all the other benthic consumer groups, except bacteria) and detritus (labile and refractory).

Figure 1.3: Map of the world showing the bays used to evaluate the performance of the Integrated Generic Bay Ecosystem Model (IGBEM). Boxes mark the locations of all the systems for which marine biomass or production estimates are available for comparison with the output of IGBEM. The solid black boxes indicate systems for which complete biomass data are available. The inserts are maps of the particular estuaries or bays that were used to set the level of nutrient inputs for the test runs, they were: (A) Port Phillip Bay, (B) Cochin Backwater, (C) Firth of Clyde, (D) Flax Pond, (E) Chesapeake Bay, (F) Apalachicola Bay and (G) San Francisco Bay. The scale bar in each case represents 10km, Flax Pond has no scale bar as its total length (west to east) is approximately 600m. The two bays with a bold border (Chesapeake and Port Phillip Bay) have enough available information to allow for an intensive evaluation of the runs.



Biomasses

Empirical estimates of average biomasses for the trophic sets covered in IGBEM were obtained from the literature for 276 coastal marine systems (Figure 1.3; a list of the values and associated references is given in Appendix A). Estimates of the biomass of all major trophic sets is available for only 10 of these locations (black squares in Figure 1.3) and complete information of both inputs and the biomasses of the trophic sets is available only for Chesapeake Bay and PPB (inserts with bold borders in Figure 1.3). Thus the published values allow a very general consideration of model output across the various nutrient loadings, but a specific evaluation of performance is only possible for the case of baseline inputs (equated with PPB) and a tenfold increase in inputs (equated with Chesapeake Bay). Note that, there are insufficient data on the biomass of bacteria to include them in the general comparisons of biomass. The information that could be found shows that the values for biomass given by IGBEM for the pelagic bacteria are high and the values for the sediment bacteria are very low, something the model has inherited from ERSEM (Baretta-Bekker et al. 1995).

Range in biomass

Overall the model conforms well with the range of values seen in real systems, but the level of performance is not consistent across all measures or trophic sets. The biomass of each trophic set (Figure 1.4) is within the range of data from real bays. The model ranges are often smaller than the ranges from field data, but this is understandable given the small subset of possible nutrient inputs used (30x present loading was the highest loading used in model runs, but real inputs in some bays would reach as high as 1000x present loadings) and the use of geometry of a single bay (whereas the empirical data derive from bays of various topographical forms, from open coastal bays and shallow lagoons to deep, narrow fjords). Even though the model is of a

temperate bay, the sparse nature of empirical data for some trophic sets necessitates including data from tropical systems in the field data ranges. This would have little or no effect on the absolute ranges given for the field data for any trophic set with the exception of the fish (the maximum value would fall to 21.16 g AFDW m^{-2} if only data from temperate bays is included).

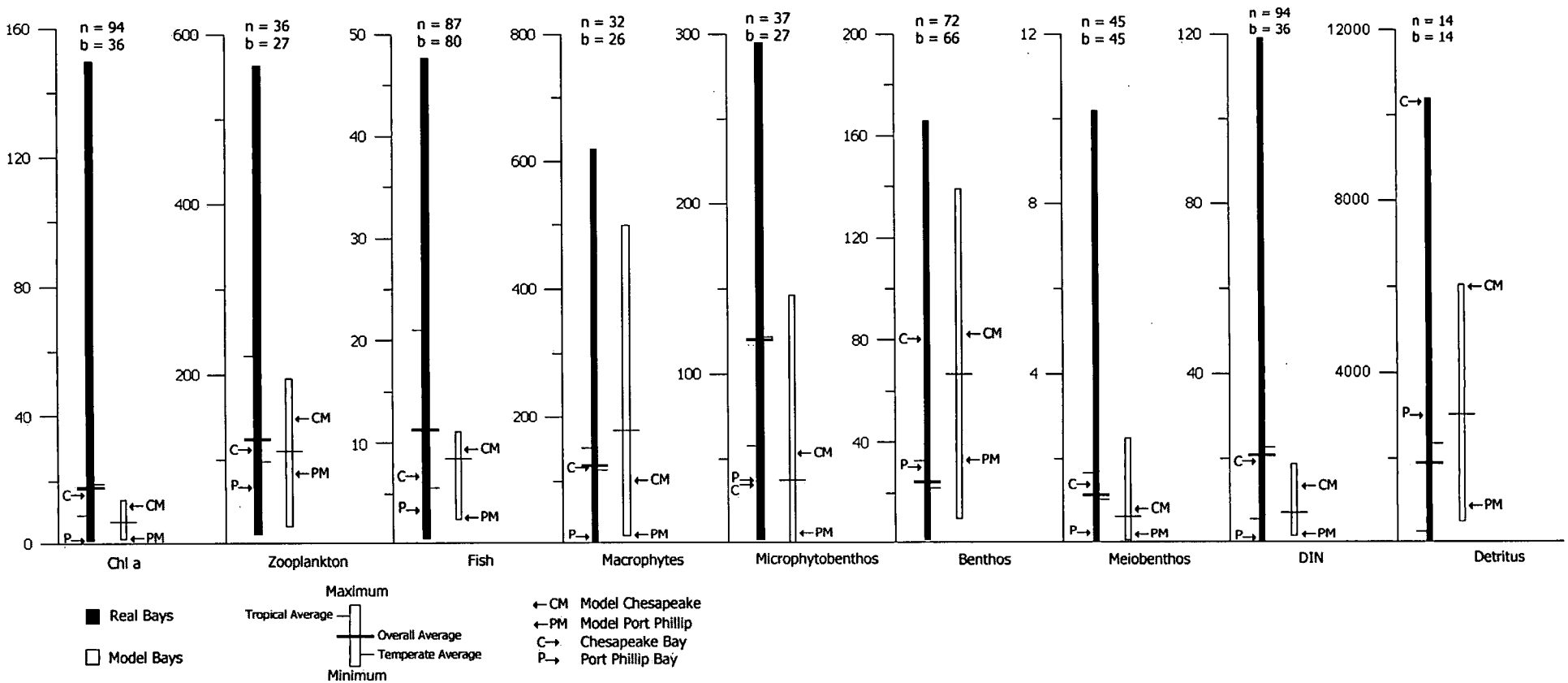
Average biomasses

The average biomasses indicate a more mixed, though still positive, performance. Given the magnitude of the range in field values, the average model values are not far from the average field values in most cases. Only three of the trophic sets have an average model value that is more than 10% of the range away from the average empirical value. Considering only the temperate average, the difference between the model and field average is 27% of the range for the benthic trophic set, 29% for the microphytobenthos and 13% for the DIN. The model also consistently yields detrital biomasses that are too low. That IGBEM does not include extremely refractory detritus, whereas the field data may, might account for this in part. However, it is also likely that estimates of the atmospheric component of detrital inputs to PPB are too low so overall inputs are too low (by about a third). Moreover, assimilation rates by deposit feeders are poorly known and may also be too high in the standard parameterisation; similarly, the burial of detritus out of the model system may be too fast.

Model biomasses in comparison with those of Port Phillip Bay and Chesapeake Bay

When the specific empirical values for the trophic sets in PPB and Chesapeake Bay are compared with the appropriate model values, the estimates for trophic sets from the model are usually within the bounds of empirical interannual variation, with the

Figure 1.4: Ranges and average values for the main sets of the model (IGBEM) in comparison with field values worldwide. The systems giving the maximum and minimum for the field data for each set are marked beside the reference in Appendix A. The model values come from the runs under different nutrient inputs based on inputs for real bays (A-G in Figure 4). The y-axis for zooplankton is Biomass in mg AFDW m^{-3}; for fish, macrophytes, benthos, meiobenthos and detritus the y-axis is biomass in g AFDW m^{-2}; the y-axis for chl a is mg chl a m^{-3}; for DIN it is mmol DIN m^{-3}; and for microphytobenthos it is mg chl a m^{-2}.



exception of the microphytobenthos and detritus. These trophic sets do not realise values within field measured levels of interannual variation and they are the only trophic sets where the difference in averages (model vs field) is more than 10% of the range in field values. The values for microphytobenthos are too low for the "Port Phillip Bay run" (PM), though it was at an acceptable level for the "Chesapeake run" (CM). There is also some suggestion that the predicted change in biomass of microphytobenthos with eutrophication is opposite to that observed empirically. The model average rose while the field values dropped marginally, if at all, given interannual variation in field values.

Microphytobenthos is the only component in the model that fails to follow the patterns of change with eutrophication that are predicted by field observations. The low levels of microphytobenthos in the baseline (PM) run are, at least in part, the result of two things. Firstly, this group competes with the large macrophyte pools, particularly the macroalgae. This causes it to be confined to the deep central parts of the bay, which have low light levels at the sediment surface. While low light levels in this area limit the microphytobenthos pool, limitation is not as pronounced as for the other benthic primary producers (the microphytobenthos light saturation is set at 3 W m^{-2} compared to 5 W m^{-2} for macroalgae and 60 W m^{-2} for seagrass). Also, as a result of very little available information on benthic interactions, the availability of the microphytobenthos to the deposit feeders and meiobenthos seems to be set too high. The efficiency of deposit feeders mentioned above exacerbates this problem. As a result of these factors the microphytobenthos is kept cropped to low levels. This facet could be improved by further calibration of the microphytobenthos part of IGBEM. However, more importantly, all aspects of the infauna and benthic microfauna in this, and other biogeochemical models (Silvert 1991), would benefit from an increased understanding of benthic interactions and ecology.

Community composition

Another biomass related comparison that can be made for the PM run is the relative make-up of the fish and benthic communities (Table 1.5). This level of detail was only accessible for PPB and so it is not possible to repeat the comparison for the runs under altered nutrient conditions. For both fish and benthic communities the relative compositions are similar to the community compositions observed in the field and well within the bounds required for "a generic system" status for the baseline run of IGBEM. However, with regard to the specific "fit" of the predicted communities to PPB, there is room for improvement.

Table 1.5: Comparison of the community composition for the benthic and fish communities determined from empirical estimates in the real Port Phillip Bay (PPB) (calculated from data in Wilson et al. 1993) and the PM model run. Bracketed values for the fish groups in PPB are the percentages when the relative community composition is restricted to the species used to parameterise the dynamic fish groups in IGBEM.

Functional Group	**PM (model) (% of total biomass)**	**PPB (empirical) (% of total biomass)**
Fish Community		
Planktivores	46.1	18.8 (31.2)
Piscivores	13.6	5.1 (8.5)
Demersal Fish	36.1	72.0 (50.3)
Demersal Herbivorous Fish	4.2	6.0 (10.0)
Benthic Community		
Macrozoobenthos (Epifaunal Carnivores)	4.3	1.1
Benthic (Epifaunal) Grazers	4.5	4.3
Benthic Suspension Feeders	45.8	50.0
Infaunal Carnivores	11.4	6.3
Benthic Deposit Feeders	34.0	38.3

The relative values for the fish community indicate that the IGBEM run over-emphasises the pelagic component of the fish community. However, the estimates of biomass for the pelagic groups in PPB are only tentative as the fish stocks of the bay have been primarily evaluated with trawls (which catch few if any of the pelagic

species) and so the currently available estimate of the relative contribution of the planktivores to the PPB community may be an underestimate. Further, the dynamic fish groups in IGBEM do not represent the entire fish population, but only part of it. One of the static closure terms imposed on the fish groups represents sharks and other large demersal fish. If the relative composition for PPB is recalculated, based only on the species-groups (for instance flatfish rather than all demersal fish) used to parameterise the fish groups dynamically included in IGBEM, the two compositions are much closer (bracketed values in Table 1.5). There is still an over representation of the pelagic groups at the expense of the demersal groups, but the model values are much closer to the field values. Thus, if the model is judged only on those groups it represents dynamically then the trophic compositions produced by IGBEM do compare favourably (though not perfectly) with those observed in PPB. However, as discussed below, the fish groups are one of the weaker parts of IGBEM and it may well be that the standard seed populations used do not produce the correct community composition in this case.

In contrast to the fish community, the relative composition of the benthic community in IGBEM is close to that observed in PPB (Table 1.5). There is some suggestion that the model may tend to favour the traditional primary production based food web over the detritus based web that dominates in PPB. This is indicated in that the contribution of both of the carnivorous groups is higher (by more than a factor of two), while that of the suspension and deposit feeders is slightly lower, in the PM run than in PPB. This tendency may be the product of two factors. Firstly, the static loss term imposed on epifaunal groups (to represent predation by fish groups not dynamically included in IGBEM), may not be high enough in the standard parameterisation to completely capture the benthic community structure observed in PPB. Secondly, there may be a mechanism in nature that influences the population dynamics that is not present in IGBEM. For example, some kind of burrow effect may

be appropriate (as it would lessen the impact of anoxic conditions in the sediment). Alternatively an index of habitat type (like the % of the area made up by hard substrata) may be necessary so that epifaunal groups restricted by crowding and available habitat in the wild are not inflated by the large homogeneous polygons used in the model. Nevertheless, the community compositions produced by the model are adequate with regard to IGBEM's role in generating data for a wider model study.

Standard relationships

While a good fit to biomasses across many trophic sets and under varying conditions is a positive attribute, it is not sufficient given that IGBEM is the foundation of a wider investigation of model structure and behaviour. Thus, the model output was checked to see if it complied with existing patterns and relationships observed generally in the field.

The work by Monbet (1992) indicates that there is a strong relationship between mg chl a m^{-3} and mmol DIN m^{-3} in the water column. As a further test of model performance the values of chl a versus DIN for the model runs under varying rates of nutrient forcing are plotted against values from real bays (Figure 1.5) (references for the real bays are in Appendix A) to examine whether the model conforms with the observed relationship. Only microtidal estuaries and bays (tidal range < 2m) are used in this comparison since PPB (and thus the model) is a microtidal system and Monbet showed that, relative to microtidal estuaries, macrotidal estuaries have much lower concentrations of chl a for the same levels of DIN. All of the model points sit well within the general relationship between chl a and DIN observed by Monbet (1992). On a more specific level the model values are compared against the values from the bays used to set the nutrient input levels for the various test runs (Figure 1.6). This serves to reinforce the strong performance of the model in this aspect, as all of the values are

within interannual variation measured in real bays.

Figure 1.5: The relationship between the mean annual concentration of dissolved inorganic nitrogen (DIN) and chlorophyll a (chl a) for real (open circles) and modelled (solid black circles) microtidal marine systems. See Appendix A for references used to give values for real bays.

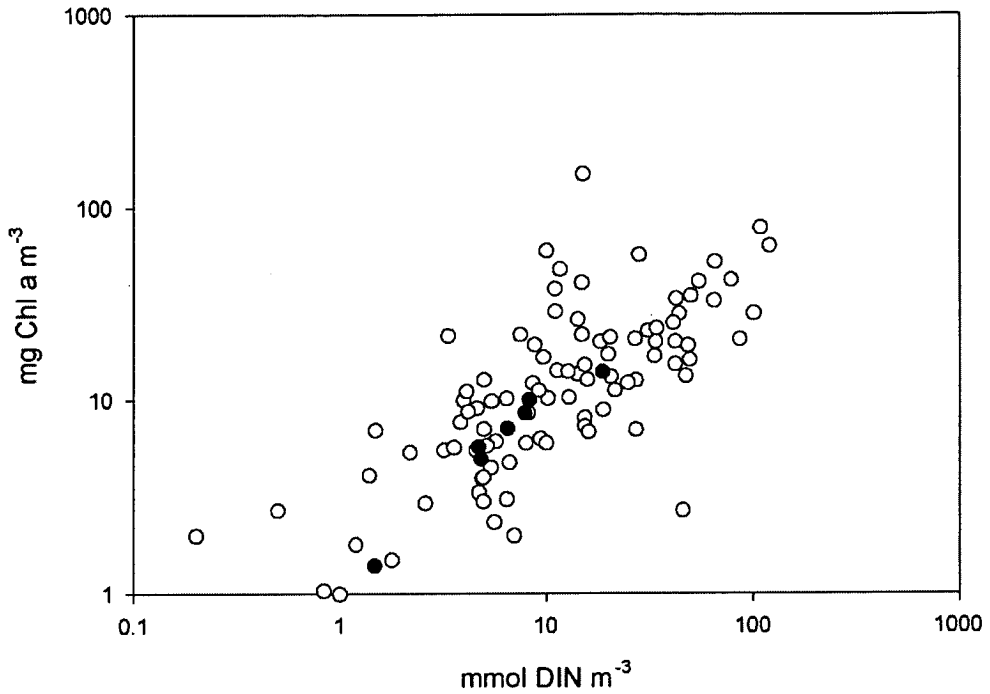
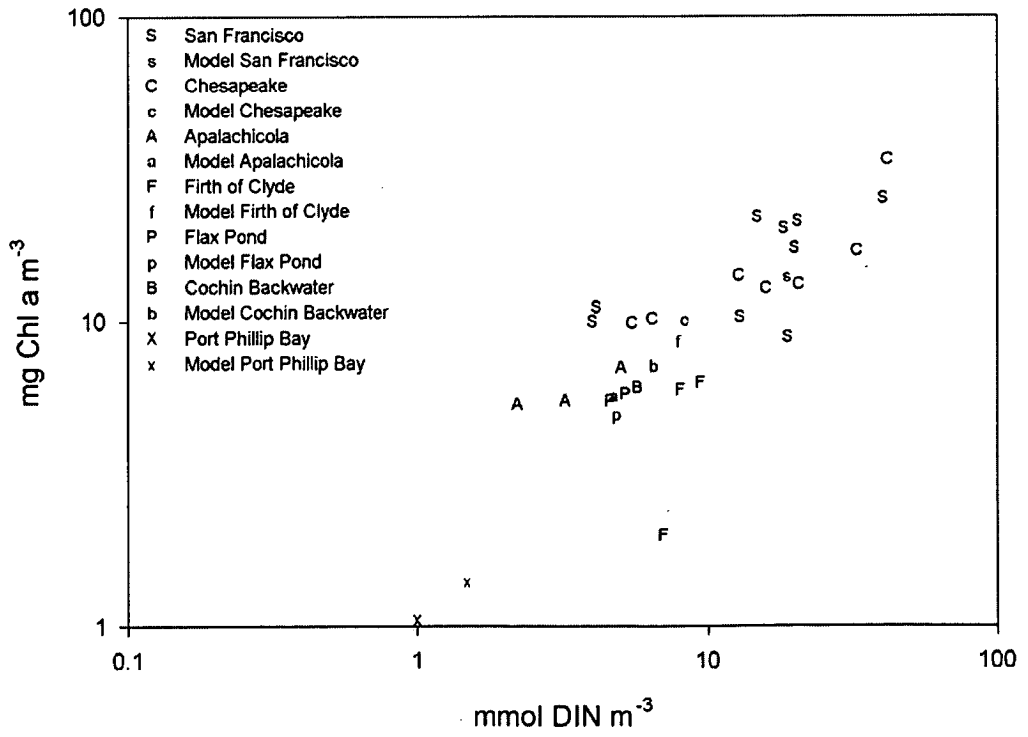


Figure 1.6: The relationship between the mean annual concentration of dissolved inorganic nitrogen (DIN) and chlorophyll a (chl a) for a selection of real and model microtidal marine systems. See Appendix A for references used to give values for real bays.



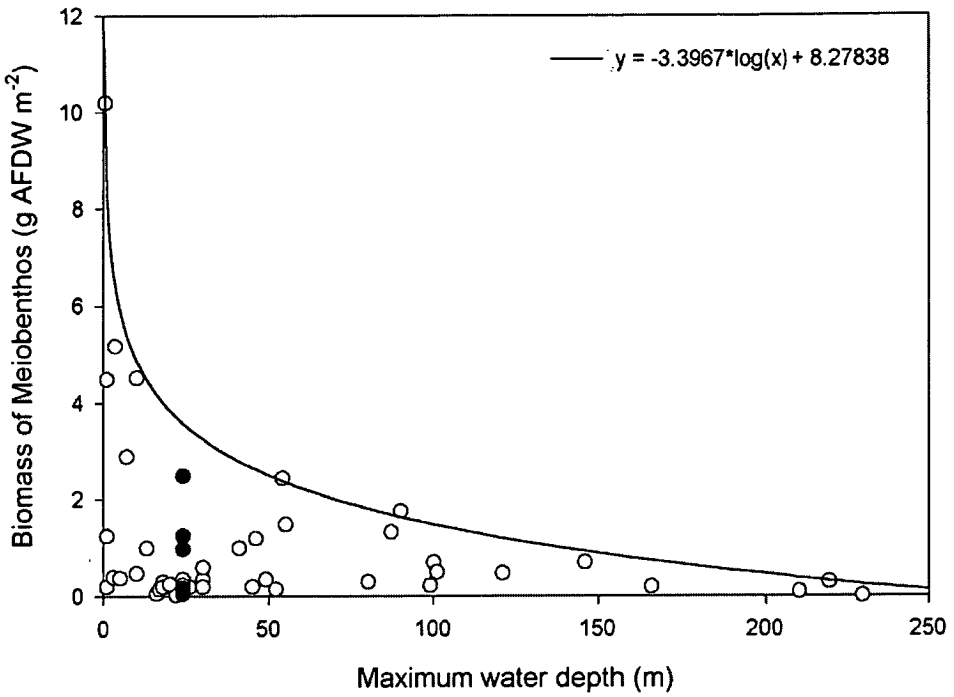


Figure 1.7: Relationship between the maximum depth and the average biomass of meiobenthos in the sediments of real (open circles) and modelled (solid black circles) coastal marine systems. See Appendix A for references for the real bays.

A general property to emerge from the empirical data is a curvilinear upper bound on the rate of decrease of the biomass of meiobenthos with increasing water depth. A curve fitted to the highest points in the plot (marked by a solid line in Figure 1.7, equation for the line given on the plot) gives an r^2 of 0.97. The model output was examined to see if it complies with this requirement (solid points in Figure1.7). As all the model points fall below the bound, it is judged that the model conformed with this relationship.

Beyond the relationships between certain groups and physical characteristics of a system, there are also relationships between relative biomasses within the biological components of systems. In marine systems two such relationships are the biomass spectrum, in logarithmic size classes, for benthic and pelagic communities. Sheldon et al. (1972) observed that marine pelagic communities appear to have similar biomasses

in all logarithmic size classes of organisms. That is the "Sheldon spectrum" is almost flat. In contrast, benthic communities have a "Sheldon spectrum" that is W-shaped (Schwinghamer 1981). Sheldon spectra for the benthic and pelagic components were obtained from the model and compared to observed empirical spectra. The spectrum for the pelagic components of IGBEM (Table 1.6) indicates that the model output does hold with Sheldon's finding that, over the entire size range of pelagic organisms, concentration varies by only an order of magnitude. Constructing the "Sheldon spectrum" is not simple for the benthic groups in IGBEM because the definitions of the groups are primarily trophic with only minor concessions to size structure. As a consequence it is necessary to use the totals per class (bacteria, microalgae and meiofauna, macrofauna) given by Schwinghamer rather than the specific values per size interval (converting the form or the "Sheldon spectrum" from a "W" into a "U"). In this case the spectrum (Table 1.7) indicates that the model does not conform well with field observations and that, using Schwinghamer's relationship as a guide, the smallest fauna in IGBEM (particularly bacteria) are under represented. The two larger classes (meiofauna/microalgae and macrofauna) are within the bounds given by Schwinghamer, but the bacteria are <2% of the field average.

Table 1.6: Summary of the Sheldon spectra for the pelagic classes in the run where nutrient loads were at the levels recorded in Port Phillip Bay (PM run) and Chesapeake Bay (CM run).

Class	PM (cm^3/m^2)	CM (cm^3/m^2)
Bacteria	40.5	149.3
Phytoplankton	10.0	75.6
Zooplankton	10.5	18.5
Planktivorous fish	5.5	23.3
Other (larger) fish	6.4	19.9

Table 1.7: Summary of the Sheldon spectra for the benthic classes in the baseline (PM) and nutrient load x10 (CM) runs of IGBEM. As a guide, the total mean biomass for each class after Schwinghamer (1981) are also provided.

Class	PM (cm^3/m^2)	CM (cm^3/m^2)	Schwinghamer (cm^3/m^2)
Bacteria	0.2	1.4	80.1
Meiobenthos and Microphytobenthos	0.7	4.3	6.1
Macrofauna	149.5	373.2	473.0

Production and consumption

Levels of daily production and consumption were obtained from the literature for comparison with the predicted values from IGBEM. Generally the model values compare favourably with the empirical field values of Production / Biomass (P/B) and Consumption / Biomass (Q/B) (Table 1.8), with some noteworthy discrepancies. Macrophyte production in the model is only a half of the field values and no easy explanation can be found for this. It may be due, at least in part, to a "macrophyte-barrens" which establishes itself in this particular run. This cycle is essentially a predator-prey cycle between the macrophytes and the benthic grazers, facilitated by the spatial and trophic structure of the model, and is discussed more fully below. Consideration of the fish on an individual functional group level rather than an overall pooled "fish" basis indicates that the P/B for the planktivores is much lower in the model output than given by the field estimates. Evaluation of the benthic components based on their habitat (epifauna vs infauna) rather than a single pooled value for all the benthos, also indicates some differences between the model and field estimates (Table 1.8). It is interesting to note that those P/B values that are considered to be substantially different between the field and the model show no consistent pattern, whereas Q/B values of the model are almost always lower than the field estimates. This suggests that while there may be multiple causes for the differences in production, the low consumption estimates are probably all due to assimilation being too efficient.

A final production related comparison is possible. The growth curves for the fish groups in the model were compared with those of real species used to parameterise the model groups (Figure 1.8). The growth curve for the individual planktivores and the herbivorous demersal fish are close matches to those for pilchards and mullet respectively. The curve for the piscivores is also a good match for the growth curve of barracouta and only the growth curve of individual demersal fish fails to fit its real-life equivalent (flathead) closely, falling short in the older fish. These older demersal fish have a diet that is primarily fish-based rather than invertivorous, and they experienced competition with the smaller piscivores. While further tuning would improve the match between the curve for the demersal fish group in IGBEM and flathead, the standard parameterisation is retained for the purposes of the wider model study as it adequately represents a demersal fish, even if it does not exactly match flathead.

Table 1.8: Estimates of primary and secondary production and consumption for Port Phillip Bay (PPB) and the PM run of the Integrated Generic Bay Ecosystem Model. Values for fish and benthos represent the pooled production or consumption value over the pooled biomass value.

Set	Production:Biomass		Consumption:Biomass	
	PPB (empirical)	PM (model)	PPB (empirical)	PM (model)
Phytoplankton	210.3	241.8	-	-
Zooplankton	2.1	1.8	3.4	2.9
Fish	3.1	4.0	21.7	13.5
Planktivorous	6.3	3.2	82.6	22.4
Piscivorous	2.0	2.6	8.2	5.9
Demersal	1.5	2.1	7.1	5.7
Demersal Herbivorous	1.2	3.1	9.6	7.0
Benthos	14.2	17.0	49.0	44.1
Epifauna	9.9	5.3	17.3	8.7
Infauna	17.6	31.1	85.1	86.6
Macrophytes	22.6	12.4	-	-
Microphytobenthos	6.3	5.2	-	-

System indices

Given the holistic nature of ecosystem studies, simple reductionist comparisons of biomasses, productivity and other ecosystem attributes are far from a sufficient summary of model performance. The fit of the model dynamics to system-level indices must also be considered. To this end a number of system indices were calculated for the baseline (PM) and nutrientsx10 (CM) runs of IGBEM. The most informative of these (based on the findings of Christensen 1992) were compared with values for the same indices calculated for 9 real marine systems (Table 1.9). The comparison indicates that the model conforms well with the real systems. For most of the indices the values for the model runs are within the range of the values calculated for the real systems. The value for the total throughput for the CM run is beyond the range given by the real bays, but this may be because the run is under a higher nutrient load (and is more eutrophic) than any of the real systems being considered.

On a specific level only 4 of the 11 indices given show a relatively close match between the values calculated for the PM run and PPB. The "System Omnivory Index", "Dominance of Detritus", "Path length" and "Relative Ascendancy" all suggest the real and modelled systems are quite similar, while the remaining indices suggest divergences. Much of this is due to the species used to parameterise IGBEM. The standard parameter set is based primarily on northern hemisphere species (as they make up the bulk of available information) and while the resulting model system does match the levels of biomass and productivity reported for PPB reasonably well, it does not do a consistently good job of matching higher level indicators. If the species used to set the parameter values are those resident in PPB, then the match between model and real system indices is vastly improved. The "BASE run" in Table 1.9 is based on parameters determined from species resident in PPB and the match between the model and real values is close for all but two of the 11 indices. Thus, the standard parameter set does a

Figure 1.8: Growth curves for fish groups as produced by the model (open circles) and the species their parameterisations are based on (solid black circles). (a) Pilchard *vs.* IGBEM planktivore, (b) Barracouta *vs.* IGBEM piscivore, (c) Flathead *vs.* IGBEM demersal, and (d) Mullet *vs.* IGBEM demersal herbivore.

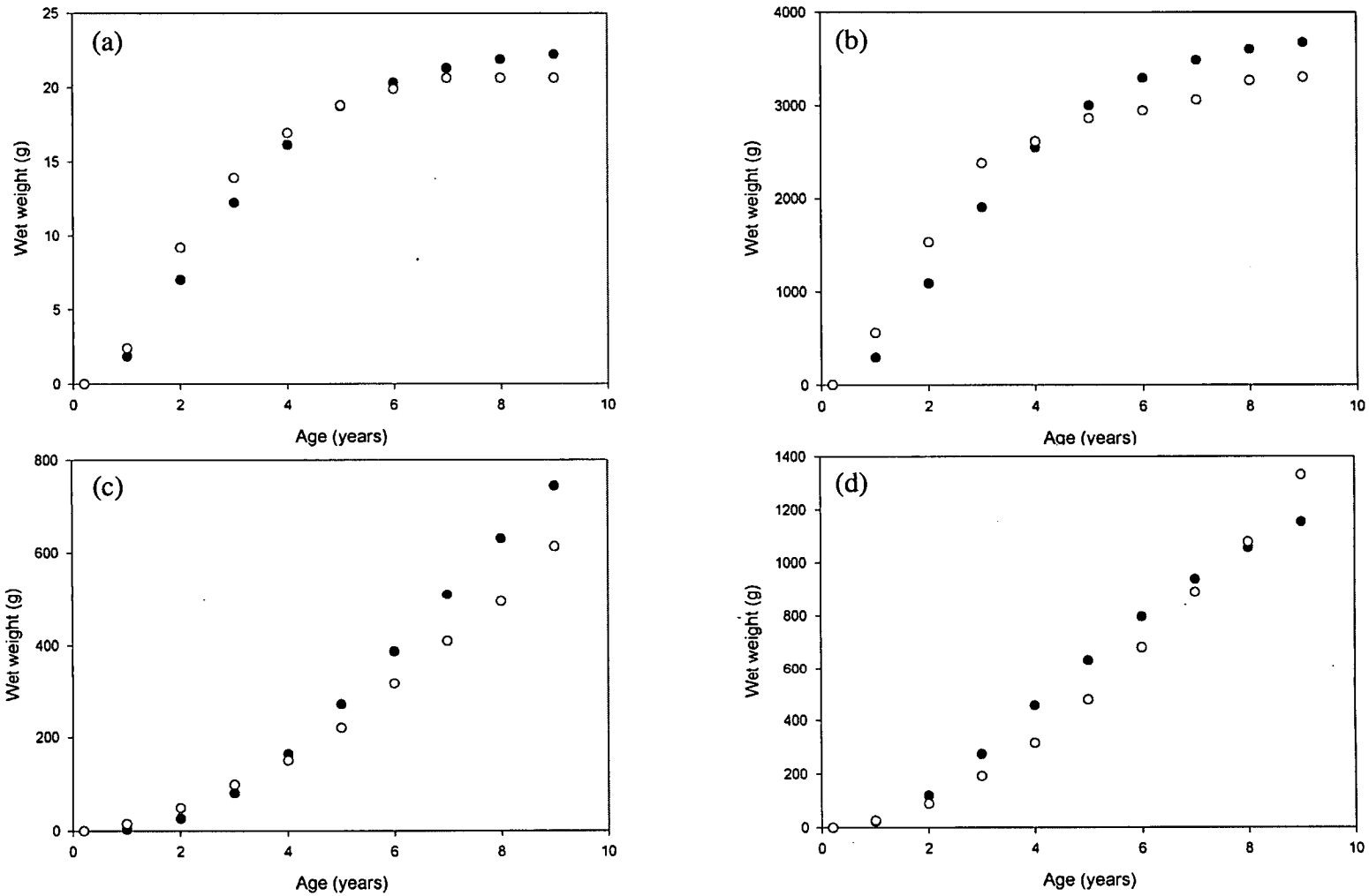


Table 1.9: System-level indices for a range of real coastal areas (values for the first 8 locations are from Christensen 1992) and three separate runs of the Integrated Generic Bay Ecosystem Model (IGBEM).

System (or run) \ Index	Sum of flows (Throughput)	Primary Production / Biomass	Biomass / Throughput	Biomass Supported	System Omnivory Index	Dominance of Detritus	Average organism size	Path length	Residence Time	Schrodinger ratio	Relative Ascendency
Mandinga Lagoon, Gulf of Mexico	3075	36.6	0.008	0.016	0.26	0.36	0.023	2.98	0.02	27.31	36.0
Tamiahua Lagoon, Gulf of Mexico	1444	9.6	0.018	0.041	0.13	0.65	0.076	3.16	0.06	14.62	25.4
Coast, Western Gulf of Mexico	17191	5.8	0.018	0.052	0.15	0.78	0.100	3.56	0.07	13.56	31.4
Campeche Bank, Gulf of Mexico	10327	5.5	0.042	0.08	0.21	0.49	0.124	3.28	0.14	7.01	26.2
Shallow area, South China Sea	11895	74.9	0.004	0.008	0.27	0.42	0.010	3.26	0.01	52.03	21.7
Lingayen Gulf, Phillipines	7198	14.6	0.013	0.037	0.15	0.63	0.041	5.14	0.07	12.46	31.1
Etang de Thau, France	41929	5.1	0.045	0.099	0.35	0.72	0.123	4.26	0.19	5.06	30.6
Schlei Fjord, Germany	2825	3.9	0.071	0.151	0.03	0.45	0.198	3.63	0.26	2.79	32.1
Port Phillip Bay, Australia	13956	14.1	0.016	0.033	0.18	0.64	0.053	4.00	0.06	16.00	32.3
BASE run (IGBEM tuned to PPB)	13243	13.7	0.023	0.053	0.18	0.49	0.049	3.60	0.08	5.15	32.5
PM run (IGBEM baseline nutrients)	4702	4.6	0.051	0.13	0.14	0.62	0.128	4.21	0.21	3.16	32.3
CM run (IGBEM nutrients x10)	50702	18.7	0.019	0.04	0.15	0.47	0.0418	3.36	0.06	4.59	29.8

sound job of reproducing a generic coastal system while tuning can produce a close fit to the holistic form of a specific system.

1.4.B Spatial and temporal form of meso- and eutrophic runs

To complete the evaluation of the standard behaviour of IGBEM, the spatial and temporal dynamics are considered. This indicates that the model can produce a rich collection of responses, from competitive exclusion to predator-prey cycles and the formation of identifiable communities structured by biotic and abiotic factors.

Spatial structure

The predicted average biomasses per box over the final four years of the CM and PM runs were analysed to determine whether there were spatial patterns in the model output. The average biomasses of all groups in each box were compared on a two-dimensional non-metric Multidimensional Scaling (MDS) plot derived from a Bray Curtis similarity matrix to identify groups of boxes of similar community structure. The average values of the physical variables and the biomass per group were examined (using the SIMPER routine of the Primer software package) to ascertain which groups determined the clustering. This analysis identified "areas" (boxes in the model sharing biological and/or physical characteristics) in the model output. Only the PM and CM runs were analysed in this way as they were considered representative of the "mesotrophic" and "eutrophic" states of the model output.

Fourteen biological areas (Figure 1.9a) and twelve geophysical areas (Figure 1.9b) exist in the output of the PM run. While there is some correlation between the two, the two sets of areas differ sufficiently that physical factors alone do not produce the form of the biological areas. Biological interactions are also important to the spatial patterning. For instance, certain functional groups consistently occur together with high

biomasses in the same cells, and these are called communities (Table 1.10). A comparison of the communities and attributes per biological area (Table 1.11) shows that Swan Bay (area 4) and Corio Bay (area 9) are distinct to the main bay. This is due to their shallow depth, large macrophyte communities and restricted connection with the main bay. Within the main bay a comparison of the biological areas reveals a depth-based zonation. The areas around the edge of the bay (areas 1 – 10) are usually distinguished by the presence of either one of two planktonic communities, as well as rich fish, epibenthic and macrophyte assemblages. In contrast the deep central sections of the bay (areas 11 – 14) all share a common planktonic community and the macrobenthic groups are largely replaced by microscopic communities able to tolerate the low light while exploiting the high levels of detritus. There is some seasonal and interannual variation in the composition of the communities and some switching between specific plankton communities expressed in the areas along the bay edge, especially within the planktonic communities 1 and 2. This is mainly as a result of responses to tidal forcing and the patterns of nutrient forcing within and across years. Nevertheless, the overall differences between the central and edge areas persists over time in the model output.

Figure 1.9: Maps of the location of the physical and biological areas identified in the output of the PM run. (a) The biological areas (sections of the bay in the same "biological area" are marked with the same number), and (b) the physical areas (sections of the bay in the same "physical area" are marked with the same letter).

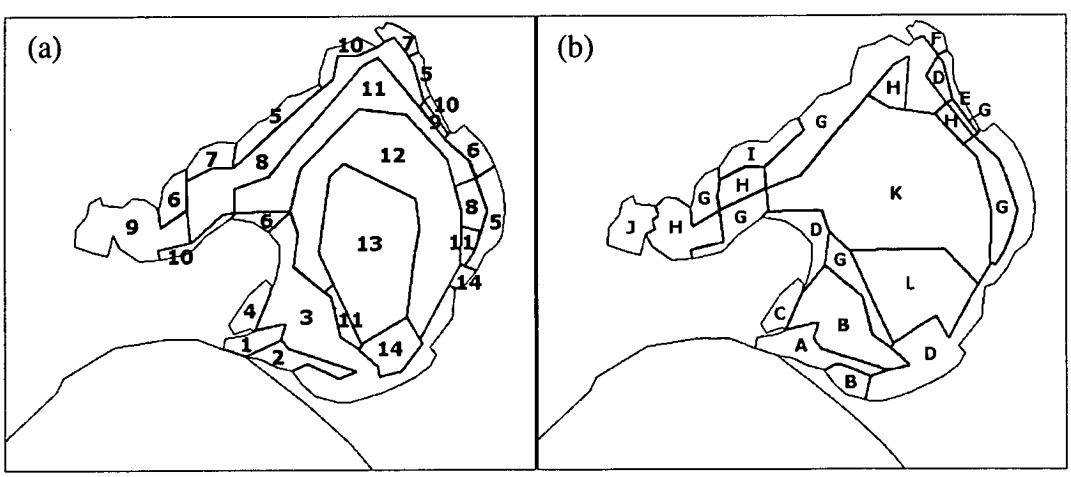


Table 1.10: Definitions for the various communities found in the output of the Integrated Generic Bay Ecosystem Model runs.

Community		Functional Groups Present
Planktonic	1	diatoms and autotrophic flagellates
	2	picophytoplankton and microzooplankton
	3	picophytoplankton, autotrophic flagellates, dinoflagellates, heterotrophic flagellates, large omnivorous zooplankton and large carnivorous zooplankton
	4	heterotrophic flagellates
Epibenthic	1	benthic suspension feeders
	2	macrozoobenthos (epifaunal carnivores)
Macrophyte	1	seagrass
	2	macroalgae and benthic (epifaunal) grazers
Fish	1	planktivores
	2	piscivores
	3	demersal herbivorous fish and demersal fish
	4	piscivores and demersal fish
Benthic	1	benthic deposit feeders and infaunal carnivores
	2	meiobenthos and microphytobenthos
Remineralisation (Remin)	1	pelagic bacteria, aerobic bacteria, anaerobic bacteria, labile and refractory detritus
	2	pelagic bacteria
	3	aerobic bacteria
	4	labile and refractory detritus

Table 1.11: Dominant communities and physical attributes characterising each biological area identified in the PM run. Codes for the functional communities are as for Table 1.10. For the biological communities a blank entry signifies that while a community of that kind may be present in the area it was not large enough (relative to their size in other areas) to significantly contribute to the definition of the area. A blank entry for a physical attribute signifies low to negligible levels for that attribute.

Area	Biological Communities						Physical Attribute				
	Planktonic	Fish	Epibenthic	Benthic	Macrophyte	Remin	Tidal Influence	Bottom Stress	Light Levels	Depth	DIN Levels
1	1	1					High	High		Moderate	
2	1,2		1				Moderate			Deep	
3		2			1			High	High	Shallow	
4					1				Very High	Very Shallow	Moderate
5	2	2	1							Shallow	High
6	2		1						Moderate	Shallow	
7	2	2,3	1,2	1		4				Shallow	Very High
8	1		1		2	4				Intermediate	Moderate
9			2		1,2				Moderate	Shallow	Moderate
10	1	1,2,3							High	Shallow	
11	3		1		2	1				Moderate	
12	3		1	2		1				Deep	
13	3		1	2		1				Very Deep	
14	3									Deep	

When the CM run is analysed only 10 distinct biological areas and 9 physical can be identified (Figure 1.10). The decline in the number of the physical areas results directly from changes in the levels of inputs and indirectly from changes in the biological components and their resultant effects on light, nutrients, detritus and bottom stress. The two sets of areas do show some overlap and the correlation is more pronounced than in the PM run, but it is still clear that abiotic factors alone are not the cause of the biological areas. As before, the mix of biotic and abiotic agents is thought to form the areas seen in the output. Once again there are clear differences between the areas along the edge and those in the middle of the bay (Table 1.12). However, the distribution of "central communities" is now much more widespread than in the PM run and they have taken over much of what was previously the domain of the "edge communities". An "edge community" still exists but it is restricted to the very edge of the northern parts of the bay. Moreover, the distinction between "edge" and "central" planktonic communities is less clear. Swan Bay and Corio Bay again stand out as being substantially different from the main bay, but the contrast is much sharper than for the PM run. Even though no functional groups disappeared from the run, some rose substantially at the expense of others which where depressed to low levels and restricted to much smaller areas. This suggests that the model is replicating the simplification of habitat and the reduction in diversity seen with eutrophication.

Temporal dynamics

Distinct temporal patterns are evident in the long-term output of the PM run, including seasonal, interannual and decadal cycles (Figure 1.11a-d). The cycles seen in fish biomass will not be discussed here as they are largely prescribed by the movement regime employed, with only minor amounts of variation occurring due to interannual variation in growth tracking their food supply (Figure 1.11e).

Table 1.12: Dominant communities and physical attributes characterising each biological area identified in the CM run. Codes for the functional communities are as for Table 1.10. For the biological communities a blank entry signifies that while a community of that kind may be present in the area it was not large enough (relative to their size in other areas) to significantly contribute to the definition of the area. A blank entry for a physical attribute signifies low to negligible levels for that attribute.

Area	Biological Communities							Physical Attribute			
	Planktonic	**Fish**	**Epibenthic**	**Benthic**	**Macrophyte**	**Remin**	**Tidal Influence**	**Bottom Stress**	**Light Levels**	**Depth**	**DIN Levels**
1	1, 4	1,2,3	1	2	1		High	High		Deep	
2		2		2				High	Moderate	Shallow	Moderate
3			1		1				High	Very Shallow	High
4	2,3	2	1,2			2				Shallow to Moderate	High
5	3	1,4	1		2	2				Shallow to Moderate	High
6	1,2	1,4	1	1						Shallow	Very High
7	1,2	4	1,2	1,2		3,4				Shallow	Very High
8			1		1,2				Moderate	Shallow	High
9	2,3		1	1,2		1				Moderate	High
10	2,3		1			1				Deep	High

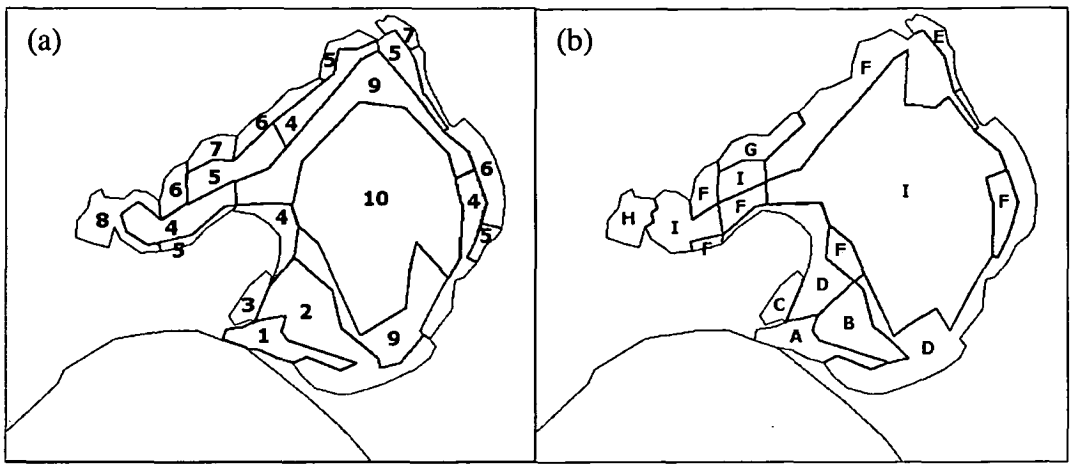


Figure 1.10: Maps of the location of the physical and biological areas identified in the output of the CM run. (a) The biological areas (sections of the bay in the same "biological" area are marked with the same number), and (b) the physical areas (sections of the bay in the same "physical area" are marked with the same letter). The letters and numbers used in this figure do not correspond to any of those in Figure 1.9.

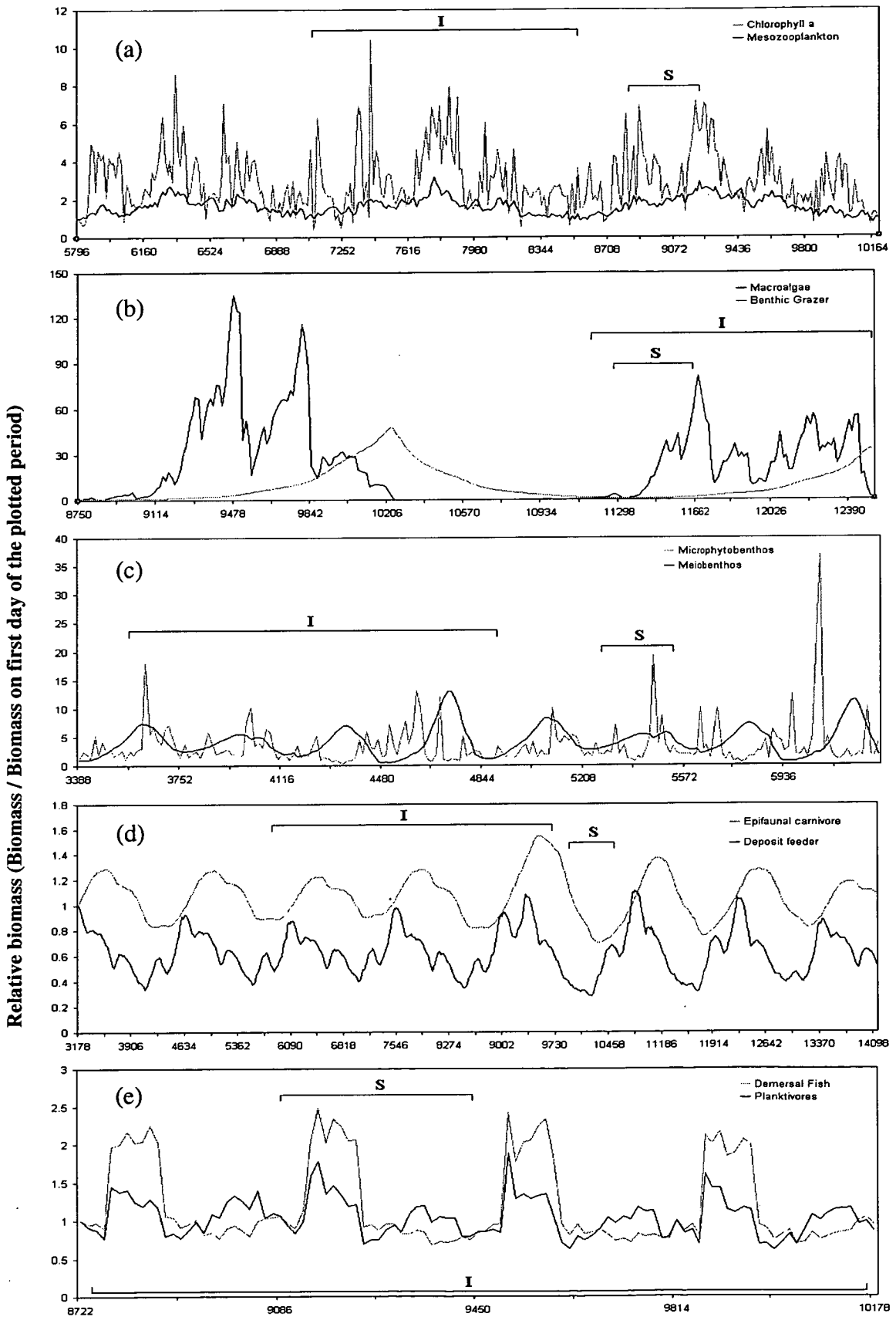
While there are high levels of short-term fluctuation in the phytoplankton groups, seasonal cycles within the planktonic groups are nonetheless clear (Figure 1.11a). This cycle is characterised by blooms in the planktonic communities associated with seasonal cycles in light levels, temperature, river flows and nutrient inputs provided by the forcing files. The build up in DIN over the winter months, particularly in the boxes fed by the two largest nutrient point sources (the Yarra River and the Werribee Sewage Treatment Plant, Figure 1.1), leads to bloom events in spring when light levels begin to rise. The form of the blooms is least stable in the Yarra and WTP boxes where local flows cause a lot of variation. Further away from the point sources, cycles are much more stable. Similar seasonal cycles can be seen in the benthic primary producers (Figure 1.11b, c) and the detritus based web fed by them (Figure 1.11d). The slow growing nature of the consumers in this set of cycles means that they show little, if any, of the short-term fluctuations which are common in the planktonic dynamics.

The looping of the hydrodynamic files (the same cycle of 4 years is continually repeated for the whole run) is apparent in the interannual variation. Many groups fall

into a steady repetition of interannual variation through time (Figure 1.11c, d) and this is due to the influence of the hydrodynamics on nutrient supply, advection of the water column communities and other food supplies. The strength of the impact of the cycle of hydrodynamic forcing differs between boxes and is strongest in the central parts of the bay, where boxes are distanced from point source inputs. The dependence of the behaviour of so many groups on the hydrodynamic cycle (either directly or via the impact of it upon their food and nutrient supplies) agrees with the findings of the developers of PPBIM (Murray and Parslow 1997) and ERSEM (Ebenhöh et al. 1995). It is interesting however, that even these cycles do not become regular bay-wide, as variation is evident in the amplitude and period of the cycles. This variation in amplitude and period would be lost within all the other forms of variation (and error) in the field, but its existence is intriguing. Apparently the extra variation is due to the effect of the point source impacts on prey groups in conjunction with the timing of the few stochastic components of the model (for example the exact day that recruitment begins in fish). The combination of bottom-up and top-down controls leads to noticeable variation in a pattern that could be expected to be extremely predictable given the cyclic nature of the forcing conditions.

The interaction of physical forcing and biotic interactions also underpins the more interesting long-term cycles (5 – 20 years). The two cycles in question are in the epibenthic groups. The first is a "macrophyte-barrens" cycle (example in Figure 1.11b) where the macrophytes are at high levels (equivalent to temperate kelp forests) for between 2 and 7 years before dropping to very low levels (<1 mg N m^{-3} in some cases) for between 2 and 9 years. The cycles have a shorter period (about 4 years for a complete cycle) in the areas with conditions conducive for macrophyte growth and are much longer (up to 15 years) in those parts of the bay with conditions less hospitable to macrophyte growth. The benthic grazers are also locked into this cycle, though the

Figure 1.11: Relative Biomass (Biomass / Biomass on first day of period shown) (y-axis) through time (x-axis) showing temporal patterns for representative groups in the PM run of the Integrated Generic Bay Ecosystem Model. The small spans marked by S are an example of seasonal variation, the large spans marked by I are examples of interannual variation. The entire period plotted in (c) and (e) are examples of decadal scale cycles. All but (d) are from edge boxes, while (d) is from the large central box.



amplitude expressed from one repetition of the cycle to the next is not necessarily constant, as it also depends on levels of their predators. This cycle may be a model artefact or a symptom of an instability as no such cycle has been recorded for PPB. However it does a very good job of simulating the impact of urchin barrens in a temperate system, a dynamic that has been widely reported and investigated (Hagen 1995, Leinaas and Christie 1996, Silvertsen 1997, Sala 1997). The whole cycle can be suppressed by adjustments to the growth rates of the main groups involved in the cycle (the macrophytes, benthic grazers and epifaunal carnivores) and by reducing the availability to predation of the macrophytes and the benthic grazers.

The other long-term cycle is related to the "macrophyte-barrens" cycle. The epifaunal carnivores show long term changes in the pattern of their interannual variation (Figure 1.11d) depending on which food web they are receiving most prey from. The amplitude of the cycle in their abundance is smaller if the detritus based web (infauna and suspension feeders) makes up most of their diet and the benthic grazers are only a relatively small part. If the contribution by the benthic grazers to the food supply of the epifaunal carnivores rises above 20% (which occurs if the barren cycle begins its decline slightly later in the year than normal) then the cycle switches to one with larger amplitudes. This cycle gradually slips back into the previous state (where the benthic grazers make up a smaller proportion of the diet) over time. These patterns (the "macrophyte-barrens cycle and the one seen in the epifaunal carnivores) indicate that long-term change in system dynamics and biomass may be a feature of systems that are under a mixture of bottom-up, top-down and abiotic control. Attempts to ascertain the impact of human actions under these circumstances would be problematic. Despite this, human actions do have the potential to cause widespread changes in system behaviour if they impact upon a crucial group or occur at a crucial time.

The patterns outlined here persist in runs with higher nutrient loadings. The

exact form and magnitude of the pattern often changes (in response to the higher levels of nutrients and eutrophication), and some change from a 4 year to an 8 year period (for example the microzooplankton in Corio Bay), but on the whole the cycles are still recognisable. The only cycle that disappears is the long-term one identified in the epifaunal carnivores. The contraction of the macrophyte community to only a handful of boxes means that the coincidence of events required to cause the change in the cycle of interannual variation in the epifaunal carnivores no longer occurs. This supports the view that anthropogenically induced changes can cause large alterations in system behaviour beyond simple reductions in diversity and shifts in biomass.

Effects of eutrophication

Monitoring studies have noted that as nutrients increase there is an initial increase in production and biomass, which is reversed (particularly in the benthic community) if the level of nutrients keeps rising (Harris et al. 1996). Studies have also shown that these changes in productivity and biomass are also associated with a general decline in species diversity and system complexity (Gray 1992). These findings are borne out in the output of IGBEM across a range of nutrient loadings.

If the various runs are considered as points along a continuum of nutrient increase, then within the water column there is a general increase in overall productivity (by a factor of five to ten) as nutrients rise. There is a concomitant change in community composition, with the larger phytoplankton and zooplankton groups dropping off and being replaced by the small rapidly growing groups. In comparison to the patterns observed in real systems suffering the effects of eutrophication, this result is not completely as expected. It has been found that as nitrogen loadings increase the composition of the phytoplankton shifts from one dominated by small cells to one centred on large cells (Murray and Parslow 1997). This is opposite to predictions of the

model where the proportion of the phytoplankton community made up by the diatoms and dinoflagellates fall by 5% with increasing nutrients in the water column. It has been very difficult to determine what changes in community compositions result with changes in nutrient levels for other ecosystem models, as results are usually given in terms of "phytoplankton" rather than specific size classes. However, the fact that ERSEM I and II consistently give ratios of small to large phytoplankton that are too high, despite the fact that field observations suggest the reverse is true for the North Sea (Varela et al. 1995, Ebenhöh et al. 1997), suggests that IGBEM has inherited this characteristic from ERSEM II. Another potential explanation is that the elevated nutrient loadings used moved the system to a state where the diatoms are silicate limited, and thus the proportional contribution of small phytoplankton increased, as predicted by Murray and Parslow (1997). In contrast with the phytoplankton dynamics, the 20% increase in the proportion of the zooplankton community made up of small size classes does match with relationships found in real estuarine systems (Park and Marshall 2000). Thus, the gross dynamics of the planktonic trophic levels in IGBEM do match field observations, but the exact form of the composition of the communities within those trophic levels are not always consistent with real systems and this suggests that the linkages and parameter values used need more consideration if the model is to be applied to a specific system for prognostic purposes.

Within the fish groups there is some increase in production and biomass (it increased by a factor of 3.5) with eutrophication, but it is not as pronounced as that in the planktonic groups. More interestingly there is a change in the average size of the demersal fish (it drops by up to 10%), so that the system is populated with more fish of a smaller size. This also concurs with observations made in the field (Tober et al. 1996). One thing to note at this point though, is that as nutrients rise to 30x baseline levels there is no collapse in the fish stocks as might be predicted based on the recruitment

failures observed in certain real systems under this level of pressure. This is due to two features. Firstly the system being modelled is shallow and vertically well mixed so there is no stratification or anoxia like that observed in the Baltic and deep parts of other coastal marine systems. As a result there is no substantial jump in the mortality of the fish groups as eutrophication sets in. Secondly, recruitment in the standard run is constant and so the population is buffered from negative reproductive impacts of the high nutrient levels.

The well-mixed nature of the model system also prevents a complete devastation of benthic groups by eutrophication-induced anoxia. However, they are not completely spared and the initial rises in productivity and biomass (to fourfold original levels) soon give way to declines (down to a third of the initial values) as conditions become increasingly stressful and the epifaunal groups all but disappear (dropping to 20% of the baseline biomass). Intense phytoplankton blooms in the water column starve the benthic primary producers of light and nutrients and so these dwindle (the seagrass density drops by an order of magnitude). A wide number of studies have observed this pattern of change with eutrophication in benthic flora (Walker and McComb 1992, Harris et al. 1996). This decrease in the benthic flora causes some reduction in the oxygenation of the sediments, though a weakness in the sediment chemistry model means that the impact of this is not as strong as it should have been. Further, it causes a drop in one of the major benthic food sources (as the benthic primary producers are food for the grazers, but also supply much of the detritus for the deposit feeders). The increase in detrital material coming from pelagic blooms more than compensates for the loss of detritus from the macrophyte groups, and so the infaunal groups increase with the nutrient inputs. It is anticipated that an improvement of the sediment chemistry model, or an application of IGBEM to a system that is deeper and not so well mixed, would see anoxia of the bottom sediments have a substantial impact on all the benthic groups. An

interesting result is that, despite the problems with the sediment chemistry model and the bacterial dynamics in general, as the levels of nutrients rise in the model the ratio of aerobic to anaerobic bacteria drops (from 2.8 to 0.14). Given that there is increasing pressure to identify reliable indicators of ecosystem health that are also easy to measure, identification of relationships such as this one could prove to be useful if they hold in the field.

No component of the model completely disappears with an increase in nutrients, but the change in relative compositions in all of the communities indicates a shift to smaller, faster growing more opportunistic groups with eutrophication. Further, as mentioned in the sections above, there is a simplification of habitat and a substantial expansion of the communities tolerant to low light, high nutrients and detritus. Thus, the model is showing a simplification of the overall system with eutrophication similar to that observed in the field (Harris et al. 1996). This agreement between the patterns of biomass, distribution of communities and productivity produced by the model and those observed in real systems indicates that the model does reproduce realistic system dynamics despite possible short comings of its current parameterisation.

1.4.C Weaknesses and alternative formulations

Closure at the top

The form of the mortality terms applied to the top-most groups explicitly represented in the modelled web is known as trophic closure or model closure (Murray and Parslow 1999b). There are a number of forms of model closure, but the two most common are linear and quadratic mortality terms and these have differing underlying ecological assumptions (Edwards and Brindley 1999, Murray and Parslow 1999b). The use of a linear term assumes that predation due to groups not explicitly included in the web is either negligible or unresponsive (does not change with the size of the modelled

group in question). Whereas a quadratic term assumes that the biomass (and resulting predation pressure) of the groups not explicitly covered by the model changes with the biomass of the modelled group. Beyond their ecological implications the two forms of model closure can lead to differing model behaviour (Steele and Henderson 1992, Murray and Parslow 1999b). The issue of trophic closure in Nutrient-Phytoplankton-Zooplankton models has received a good deal of attention (Steele and Henderson 1992, Edwards and Brindley 1996 and 1999, Murray and Parslow 1999b, Edwards and Yool 2000). However, the same level of consideration does not seem to have been given to higher trophic levels and by and large the different forms of mortality used are either constants or they are assumed to be linear and additive.

Experience with IGBEM indicates that more thought about model closure is necessary. It would be hoped that an ecosystem model could provide some insight into the pristine state of systems that have been impacted by human actions. To this end runs where there is no fishing were undertaken. Under the standard parameterisation there is some shift seen in community composition and biomasses, but the model is still stable. However, during an exploration of the parameter space it is found that if the system was set more in line with the levels of fish biomass and community composition found in places such as the North Sea then the linear closure terms are insufficient to ensure model stability. This may simply reflect the magnitude of human impact on systems such as the North Sea, and that models with fixed parameters cannot cope with the level of change such systems manifest as they return to more pristine states. Nonetheless, it can also be argued that failure to cope with the removal of fishing pressure in this case suggests that there may be potential problems with the closure of the model and that the issue of how models are closed, regardless of the number of trophic levels included, needs wider consideration. In a study comparing three ecosystem models across a range of eutrophication and fishing scenarios (chapter 7), it was found that using linear closure

terms for the predation effects caused by highest order predators may not be a suitable model of system dynamics. This is because populations of the higher predators do not change linearly with fluctuations in their major prey groups. Extension of the individual-based handling of the fish groups to include seabirds, mammals and sharks may be beneficial if only to check whether they can then be omitted. Similarly, consideration of the impact of quadratic rather than linear closure of ecosystem models may prove instructive, with regard to whether the extra parameters are justified in terms of improved model stability, more realistic model behaviour and, potentially, more realistic underlying assumptions.

Constant recruitment

It was found (chapter 7) that the constant recruitment term employed in IGBEM could have a substantial influence on the predicted impacts of eutrophication and fishing pressure. The fish groups in IGBEM are buffered against the impacts of large-scale changes in system productivity due to their constant recruitment. Further assumptions about the form of the linkages between the lower and upper ends of the trophic spectrum could have profound consequences for model behaviour. To check this, alternative recruitment formulations were trialed in IGBEM. Of the alternative recruitment relationships, the use of the Beverton-Holt recruitment relationship gives the most satisfactory result, as it displays the increases and declines with stock size and productivity that have been observed in other models (chapter 7) and in the field. Recruitment based on primary productivity requires further refinement as it does not show decline in fish stocks with eutrophication (the biomasses actually rise by a factor of 4.6 - 7.3). If this form of relationship is to be used then the relationship must be tied to specific parts of the planktonic community if realistic dynamics are to be produced. The final, lognormally distributed, recruitment relationship does not have the freedom

to respond to changes in productivity any more than does the constant recruitment term (as the parameters used in the distribution do not change). Nevertheless, it may be useful in the future for the evaluation of the effects of varying cohort strength at the system level.

Prescribed movement

The prescription of fish movement does not have a large impact on the dynamics of the model. However, the prediction of artificially high predation rates in some boxes with low productivity (and vice versa) when using prescribed movement (Bryant et al. 1995), in conjunction with theories regarding optimal foraging, led to the creation of a forage- and density-dependent based fish movement module. It was found that under this movement scheme only the planktivorous fish show movement that is a close approximation of that observed in PPB. These fish move north in the spring to take advantage of the blooms in the northern boxes, but are more generally spread during winter when they return to the southern boxes. This is largely in agreement with what is observed for the anchovies in PPB (the pilchards do not remain in the bay all year round, leaving in winter) (Gunthorpe et al. 1997). The demersal herbivorous fish show some features that resemble the seasonal movements of mullet (entering the mouth of the estuaries and bays in late summer). This resemblance is probably superficial, since mullet migrate to these locations to spawn and then return to their more standard habitats (Gunthorpe et al. 1997), whereas the demersal herbivorous fish were switching from a winter (detritus based) to higher quality summer (macrophyte) based diet and redistributing accordingly. The other two fish groups show little, if any, resemblance to reported patterns (the demersal fish are consistently homogeneously spread across the bay and the piscivores track the distribution of their major prey items). While an

intriguing beginning, this module requires more work before it shows any real advantage over the use of prescribed movement.

1.5 Conclusions

All facets of society are becoming increasingly concerned with whole systems rather than those directly affected by harvesting or pollution. As a consequence dynamic models that try to concisely capture the important aspects of ecosystems are receiving more attention (Bax and Eliassen 1990, Sekine et al. 1991, Riegman and Kuipers 1993, Baretta et al. 1995, Baretta-Bekker and Baretta 1997, Walters et al. 1997, Murray and Parslow 1999a, Walters et al. 1999, Walters et al. 2000). One specific area that is proving to be crucial is the question of model complexity (O'Neill and Rust 1979, Silvert 1981, Ludwig and Walters 1985, Costanza and Sklar 1985, Silvert 1996, Yool 1998). IGBEM was built as the foundation of a study of model complexity, to provide the "baseline" against which other models of simpler form and detail could be compared. For there to be confidence in the results of such a study it would be advantageous if the output of IGBEM resembles real temperate coastal systems. Consideration of the biomasses, productivity, temporal and spatial dynamics and the response of the model's behaviour to changes in nutrient loading indicates that, despite some weaknesses, the behaviour of IGBEM does resemble that of real temperate marine systems. The ability to reproduce real world dynamics across a range of conditions suggests IGBEM provides a sound reference for the study of complexity and the effects of formulation.

Like all models, IGBEM has its weaknesses. While it does a good job of addressing several issues that plague the models it was developed from (such as resuspension and a web-like rather than a parallel chain structure) and considerably extends the trophic coverage of its predecessors, it falls short in other areas. The

problems encountered with the sediment bacteria and nitrification-denitrification submodel indicate that it may be advantageous to develop ways of making empirical relationships more flexible with a minimum of additional formulation, rather than replacing them with equations that need an order of magnitude more parameters, interpretation and effort to validate.

Model validation and parameterisation is one of the largest constraints on the widespread use of dynamic models of substantial complexity. IGBEM requires in excess of 750 parameters, some of which are difficult to measure. While the set of standard parameters is sufficient for the representation of a generic system or the gross consideration of particular systems, it is obvious that use of IGBEM in a detailed evaluation of a specific system requires tuning it to the local conditions and taxa. Unfortunately, with such a large parameter set only the most intensively studied systems (such as PPB, Chesapeake Bay and the North Sea) can provide appropriate levels of information. Varela et al. (1995) expressed a similar concern with regard to the validation of ERSEM. While more information on marine systems is required across the board (Baretta et al. 1998), models of this level of physiological and process detail may be approaching the upper bound of what can be usefully employed. Nevertheless, the richness of the behaviour of these models may prove to be more than enough, at least for learning purposes. For example, without explicitly building them into the model, IGBEM can produce many of the behaviours observed in nature - competitive exclusion, keystone groups, spatial self-organisation, stable state changes (with and without human induced triggers) and adaptation to changes in ambient conditions. The prognostic usefulness of such large models may still be under debate, but the learning potential they provide cannot be denied.

Whether dynamic ecosystem models are used solely for learning or become an integral part of the management of marine resources, it is clear that no single set of

assumptions will suffice (Harris et al. 1996). Sensitivity analysis has become an accepted part of model construction (Jørgensen 1994), though it is commonly applied only to the parameters and not the assumptions or structures used in a model. Sampling schemes for the efficient use of computational experiments to assist in the analysis of model sensitivity have received some attention (Morris 1991). Moreover, ecosystem modelling packages such as ECOPATH explicitly acknowledge the need for sensitivity analysis through the inclusion of modules such as ECORANGER, which allows for the consideration of the implications of the levels of uncertainty associated with the ECOPATH input parameters (Christensen et al. 2000). Unfortunately, it is still largely impractical to attempt an inclusive and systematic sensitivity analysis of most models with even modest numbers of parameters. This does not mean that model sensitivity can be neglected. The judicious use of factor screening appears to be an expeditious means of identifying the most sensitive parts of the model and the exploration of the effects of the resulting restricted set of parameters is a much simpler task (Morris 1991). While not as thorough as a formal and systematic sensitivity analysis it is a necessary first step if the utility of any results are to be trusted with any significant measure of confidence. Further, in these large scale and detailed system-level models it is not only the parameter values that must be explored in this way, but the fundamental assumptions used to build parts of the models. Building a number of modules in parallel and then judging the performance and change in output that results when the different modules are employed is a sound way of identifying structural sensitivity in the model as well as identifying scenarios and options that are robust across a wide range of assumptions. This can be taken a step further if multiple models of differing types rather than just multiple modules are employed. For instance, biogeochemical models (e.g. IGBEM) and dynamic aggregate models (e.g. ECOSIM) are based on very different modelling philosophies but can be applied to the same questions (chapter 7). Nevertheless,

regardless of how it is done and whether the models are to be used as a learning or management tool, the form and structure of the models must be given careful consideration if preventable and unexpected events are to be avoided. This approach has worked well with IGBEM. The model reproduces real world dynamics quite well across a range of parameter settings and those areas where it does show some weaknesses have been identified and can be monitored, or improved.

Chapter 2 The effect of physiological detail on ecosystem models I: The generic behaviour of a biogeochemical ecosystem model

Abstract

The level of detail required to efficiently capture system dynamics in ecosystem models has not been well defined. To this end an ecosystem model of a generalised bay, Bay Model 2 (BM2), was constructed. It is a trophically diverse biogeochemical model built using the general framework from a model of Port Phillip Bay, Australia. BM2 captures the essential features of real marine systems as well as another similar but more complex ecosystem model (IGBEM), which contains much more physiological detail. It is capable of reproducing realistic levels of biomass and conforms with known ecological relationships. Novel handling of bacteria, as colonisers rather than as consumers, and the inclusion of mixotrophy for the dinoflagellates lead to more realistic dynamics for these groups. These dynamics represent a substantial improvement in predictions for these components in comparison with IGBEM. The behaviour of BM2 indicates that, with regard to capturing common system dynamics, high levels of physiological detail are not always required in ecosystem models.

Keywords

biogeochemical, model, ecosystem, ERSEM, Port Phillip Bay, IGBEM, BM2

2.1 Introduction: ecosystem models and physiological detail

The evolution of ecosystem models has seen a proclivity for increasingly detailed process formulations and model structure. The mixed success and potentially large computational demands of early attempts at highly detailed reductionist ecosystem models (Hedgpeth 1977, Platt et al. 1981) lead to a return to "simple" models during the

late 1970s through to the mid 1990s. However, with no clear indication as to the effects of complexity on model performance, the "complex model" has once again seen an upswing in support. It is clear that the effect of model complexity on model performance is an important issue begging immediate attention.

A powerful approach to the issue of complexity is to begin with a highly detailed model and make systematic comparisons with simpler models. It may seem an unusual beginning to start off with a complex model when their worth is still controversial (Hedgpeth 1977, Silvert 1996a, Murray and Parslow 1999b), but this method has been used extensively and successfully in fisheries (e.g. Ludwig and Walters 1981). Moreover, as the models discussed here were to play a part in a much broader examination of the effects of model structure, it was decided that the models needed to incorporate some of the known complexities of the real world and be amenable to, potentially extensive, simplification. Insight gained during the construction of the Integrated Bay Ecosystem Model (IGBEM), a large generic bay ecosystem model, suggested that building another process based ecosystem model that is less parameter intensive may prove useful. This enabled a study of the effects of differing forms and levels of model complexity. Thus, this paper discusses the comparison of two trophic flow ecosystem models that are both reasonably large and complex, but which contain very different levels of formulation detail (Table 2.1). IGBEM (chapter 1) is heavily based on physiological detail and explicitly represents processes such as uptake, excretion, defecation, mortality, basal-, activity- and stress-respiration. In contrast, Bay Model 2 (BM2) uses simpler assimilation and generalised handling equations, which aggregate the physiological processes into three equations – one each for growth, the release of nutrients and the production of detritus. These differences allow for consideration of the impact of the formulation of internal physiological details on marine ecosystem models dealing with multiple trophic levels.

Table 2.1: Comparison of the underlying assumptions and formulations of the standard implementations of Bay Model 2 (BM2) and the Integrated Generic Bay Ecosystem Model (IGBEM).

Feature	BM2	IGBEM
General features		
Biomass units	mg N/m3	mg/m3 of C, N, P, Si
Input forcing	nutrients and physics on interannual, seasonal, tidal frequencies	nutrients and physics on interannual, seasonal, tidal frequencies
Level of group detail	functional group	functional group
Resolution of the formulation used for the invertebrate groups	entire biomass pool of the functional group in the cell	entire biomass pool of the functional group in the cell
Resolution of the formulation used for the fish groups	biomass (structural and reserve weight) of the "average individual" for the functional group in the cell and the number of individuals in the cell	biomass (structural and reserve weight) of the "average individual" for the functional group in the cell and the number of individuals in the cell
Process related		
Bioturbation and bioirrigation	yes	yes
Consumption formulation	type II	mixed (type II, type III)
Equations	five general sets of rate of change equations used (autotrophs, invertebrate consumer, vertebrate consumer, bacteria, inanimate)	eight general sets of rate of change equations used (microautotrophs, macrophytes, small zooplankton, large zooplankton, fish, zoobenthos, bacteria, inanimate)
Formulation detail	general: only growth, mortality and excretion explicit.	physiological: assimilation, basal/ activity/stress respiration, defecation, excretion, ingestion, mortality are all explicit
Light limitation	optimal irradiance fixed	phytoplankton can acclimate to ambient light levels
Mixotrophy	dinoflagellates	none
Nutrient limitation	external nutrients determine uptake	internal nutrient ratio determines nutrient uptake and disposal
Nutrient ratio	Redfield	internal specific nutrient ratio
Oxygen limitation	yes	yes
Sediment burial	if enabled, then very low	yes
Sediment chemistry	dynamic, with sediment bacteria	empirical, sediment bacteria are a tracer only
Shading of primary producers	yes	yes
Spatial structure	flexible with the potential for multiple vertical and horizontal cells	flexible with the potential for multiple vertical and horizontal cells
Temperature dependency	yes	yes
Transport model used for hydrodynamics flows	yes	yes
Model closure		
Top predators represented by static loss terms	yes	yes
Linear mortality terms	yes	yes
Quadratic mortality terms	yes	no
Fish and fisheries related		
Age structure for the fish groups	9 age classes	9 age classes
Fishery Discards	target species only	target species only
Invertebrate fisheries	yes	no
Stock-recruit relationship	constant recruitment	constant recruitment
Stock structure	external: the reproductive stock outside the bay produces the recruits and the oldest age classes migrate out of the bay to join this stock	external: reproductive stock outside the bay produces the recruits and the oldest age classes migrate out of the bay to join this stock

2.2 Building BM2

The structure of BM2

For convenience many acronyms are used throughout this paper. They are defined when first used, but for quick reference a list of acronyms and their meanings is given in Table B.1 of Appendix B.

BM2 is a process model that tracks the nitrogen and silicon pools of twenty-five living, two dead, four nutrient, six physical components and a gaseous component (Table B.2, Appendix B). The spatial geometry is made up of 59 polygons (boxes), which correspond to the geographical form of Port Phillip Bay. The area and shape of the polygons reflect the speed with which physical variables change within particular parts of the bay (Figure 2.1). This geometry was developed for the Port Phillip Bay Integrated Model (PPBIM, Murray and Parslow 1999a, Walker 1999), which was used as a base for the development of BM2. BM2 also uses the 3 layer (water column, epibenthic, sediment) vertical resolution and daily time-step common to IGBEM (chapter 1) and PPBIM. As a result, like PPBIM and IGBEM, BM2 is driven by seasonal variation in solar irradiance and temperature, as well as nutrient inputs from point sources, atmospheric deposition of dissolved inorganic nitrogen (DIN) and exchanges with the Bass Strait boundary box. BM2 retains the bioirrigation components used in PPBIM (Walker 1997), and the enhancements made to the transport model during the development of IGBEM (chapter 1). Hence, BM2 is identical to IGBEM with regard to the physical parts of the system, with the exception that the rate of sediment burial out of the modelled sediment layer is greatly reduced based on observations made during the validation of IGBEM (chapter 1).

The major differences between IGBEM (full details of its formulation can be found in chapter 1) and BM2 are in the biological aspects of the model system (Table 2.1). During the construction of BM2 the general form of the process equations

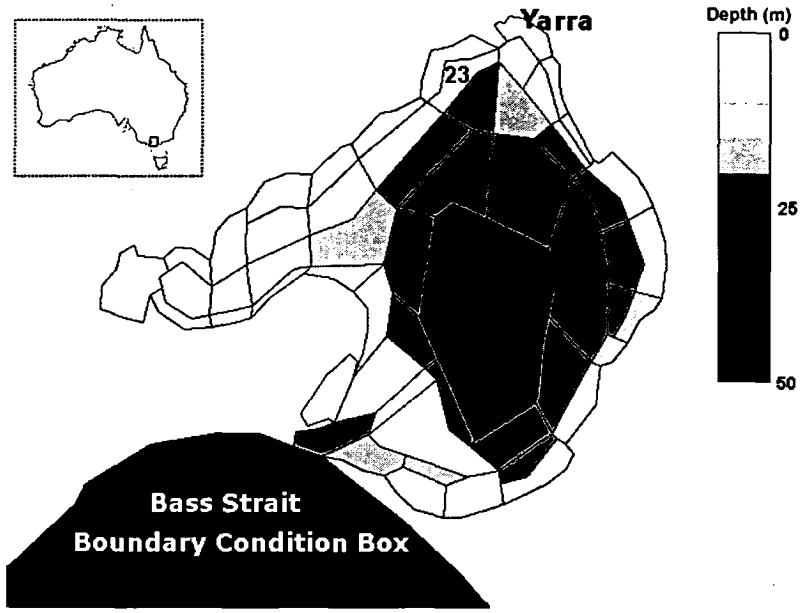
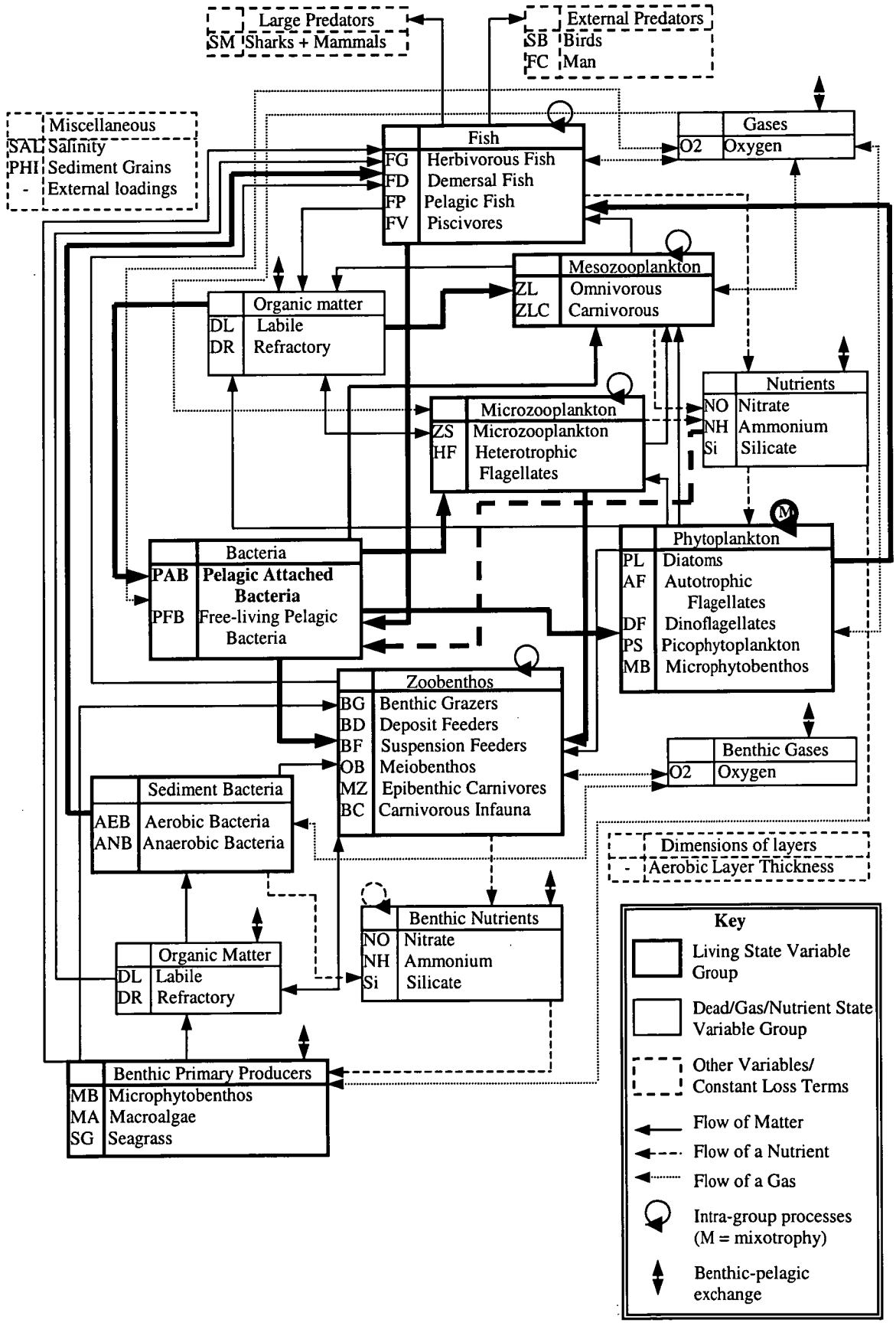


Figure 2.1: Map of the geometry used for the standard runs of Bay Model 2 (BM2). It represents Port Phillip Bay, Melbourne, Australia (location marked on map inset). The Bass Strait boundary condition box, the entry point of the Yarra River (the river the city of Melbourne is built around) and box 23 (referred to in Figure 2.10) are marked on the map.

implemented for the biological components in PPBIM (Murray and Parslow 1997) were replicated and extended (and modified where necessary) to cover all of the invertebrate groups listed in Table B.2 of Appendix B. This differs from IGBEM, which is built around a similar list of groups, but used the ERSEM 'standard organism' concept (Baretta et al. 1995, chapter 1). The fish groups in BM2 are much closer to the "average individual" model used in IGBEM, but the grazing and excretion processes are simplified to keep them in line with the level of resolution found in the rest of BM2. The general formulations for the phototrophic, invertebrate consumer and fish groups are given in Appendix C.

The groups used in IGBEM and BM2 are closely matched to allow for direct comparisons. BM2 contains a single trophic group and a small number of food web linkages that IGBEM does not (marked in bold in Figure 2.2). In BM2 the pelagic

Figure 2.2: Biological and physical interactions between the components used in Bay Model 2 (BM2). The pelagic attached bacteria and flows (arrows) in bold were built specifically for BM2 and do not appear in the Integrated Generic Bay Ecosystem Model (IGBEM). The figure is modified from that for the European Regional Seas Ecosystem Model (Blackford and Radford 1995).



bacteria are split into free and attached forms, while there is only a single lumped group in IGBEM. Since the size of the attached bacterial pool in BM2 is strongly dependent upon the water column pool of labile detritus (rather than the converse), differences in trophic structure in the models are unlikely to confound comparisons. The additional food web linkages are related to the introduction of two new processes in BM2 - mixotrophy in the dinoflagellate group and a new method of dealing with bacterial groups (particularly those in the sediment). These are two areas where IGBEM was found to be in need of improvement. Since behaviour of the entire model system is one of the most important issues in question, the benefit of adding extra linkages necessary to accommodate changes in the handling of these two outweighs the 'cost' of omitting them on the grounds of straightforward comparability with IGBEM.

Dinoflagellates are frequently represented explicitly in ecological models of the water column, but mixotrophy is not. Apart from a handful of models examining the microbial loop in detail (such as Stickney et al. 2000), mixotrophy is usually ignored in ecosystem models. In the past this reflects that little was known about it and because it was considered to have negligible impacts. However, there is now clear evidence that dinoflagellates can have significant impacts (via predation and competition) on phytoplankton and zooplankton, despite their relatively low densities and growth rates (Hall et al. 1993, Jacobson 1999). Experience gained from working with PPBIM and IGBEM suggested that some mechanism crucial in nature is lacking from standard water quality and ecosystem models. The behaviour and persistence of dinoflagellates observed in natural systems had previously proved difficult to reproduce in simulations and mixotrophy seemed a prime candidate for this missing process. The dinoflagellates in question had previously been considered pure autotrophs and, apparently, only displayed mixotrophy in the field to offset low nutrient uptake affinities, low maximum photosynthetic rates and high respiration costs (Smayda 1997, Legrand et al. 1998,

Broekhuizen 1999, Stoecker 1999, Li et al. 2000). Thus the type II (primarily phototrophic) mixotrophs from Strickney et al. (2000) were used as a guide during the formulation of the mixotrophic dinoflagellates in BM2 (given in Appendix D).

The other part of the system treated unconventionally is bacteria and their associated effects on sediment chemistry and remineralisation. Ecosystem and water quality models have traditionally treated bacteria in much the same way as all other invertebrates, using the same formulations and making only minor modifications to linkages, resource utilisation terms and parameter values. This approach is adopted for the free-floating pelagic bacteria in BM2, following the time-evolution equations for bacteria of Fasham (1993). However, a different approach is used for the three groups of attached bacteria. The growth rates of attached bacterial populations (water column and sediment alike) are equated to the availability of colonisable substrata (the detrital groups) rather than to more grazer-like consumption of prey resources. The formulations used for bacteria and their integration with the nitrification-denitrification submodel are given in Appendix E.

Parameterising BM2

The number of parameters required by BM2 is much smaller than that of IGBEM, but there are still far too many for a systematic sensitivity analysis. Consequently, the guidelines given in Murray and Parslow (1997) for the parameterisation of PPBIM were used to determine values for the majority of parameters in BM2. The final calibration of BM2 was completed by tuning the temperature-dependent maximum growth and mortality rates for all groups and the maximum clearance rates of the consumer groups, as these parameters had been identified as the most important in a factor screening. Tuning was carried out until all groups persisted and numerical stability was achieved. In the tuning procedure it was

ensured that all parameter values were within the range of empirical values found in the general literature. As a consequence of this method of tuning, parameter values did not always reflect a particular observation or reported value, but they did reflect values from the literature.

Optional submodels

BM2 is part of a wider study of ecosystem models and so many alternative submodels were built into various parts of the main model. These were generally chosen to correspond to those of IGBEM and include forage and density dependent fish movement, a fisheries effort model, fishing induced mortality on non-target groups, functional group invasions and multiple alternative functional responses and mortality schemes. The majority of these are not discussed here, but some will be addressed in other chapters (e.g. chapter 6). The submodels included here are outlined in the following section.

2.3 Model runs

The standard runs of BM2 cover a 20 year time period, with output being recorded every 14 days. This run length and record step matches that of IGBEM, and the rationale for these choices may be found in chapter 1. One hundred year runs are also undertaken to check for long period cycles and to verify that the model has reached a representative state at the end of the 20 year period. Looping of the forcing files for the physical transport model is necessary, as the files only span four years, and this is done in the same manner as for IGBEM (chapter 1). The majority of the groups in the modelled food web have a linear natural mortality term, but for those groups on the upper edge of the web an additional quadratic mortality term is also imposed. This second term represents predation due to groups not explicitly represented in the

modelled web. This combination of linear and quadratic mortality terms is used in all standard runs of BM2, and the functional response employed in these runs is the one used in PPBIM (a Holling type II). In the standard form of BM2 the recruitment of fish is constant and fish migration is prescribed (as in IGBEM, chapter 1).

The assumptions underlying the formulations for the recruitment and movement of fish are some of the weakest in BM2. Thus, to explore model behaviour under alternative assumptions, runs that used alternative fish movement and recruitment relationships were undertaken. Forced migration and constant recruitment of fish, as employed by ERSEM II, was adopted initially, and this facilitates comparisons with IGBEM. Other formulations examined included alternative recruitment formulations and a forage and density dependent fish movement, which allocates fish to the cells based on available resources, clumping around good resources and dispersing if conditions were poor (rather than a fixed, prescribed, matrix of proportions) (Appendix F). The alternative recruitment formulations include a lognormal distribution, a Beverton-Holt stock recruitment curve, and a recruitment relationship which uses primary production (as a proxy for larval resource availability) to dictate the number of recruits settling out in each cell (Table 2.2). These recruitment relationships are parameterised such that, if there is a constant stock size and no environmental changes, the average number of recruits returned matches that of the initial state of the system.

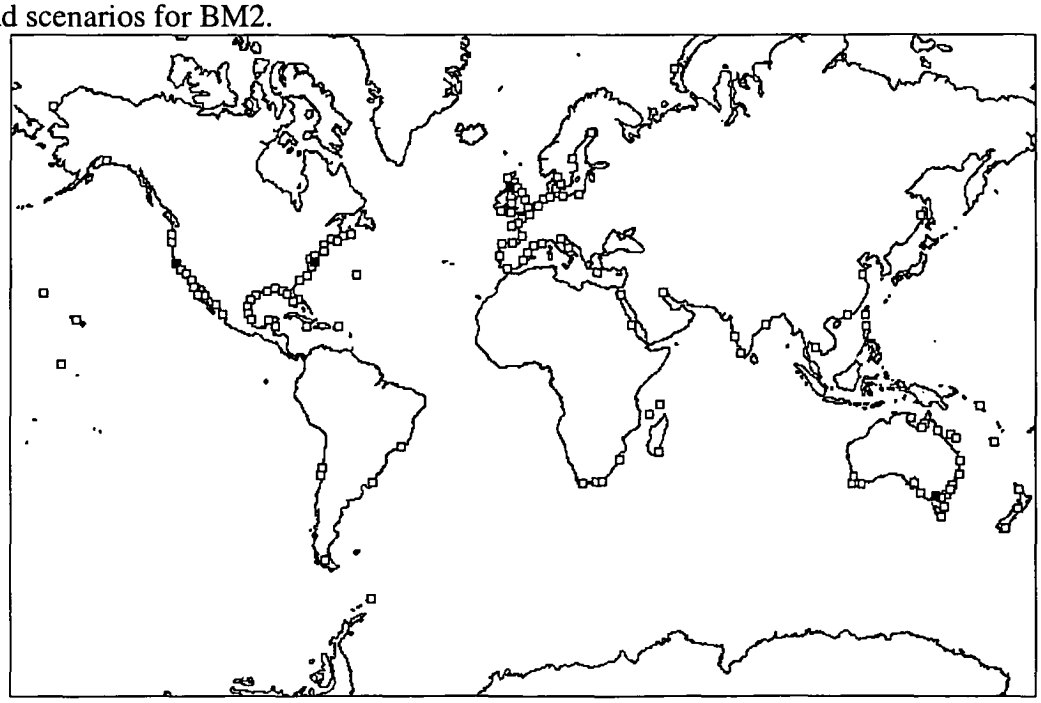
To evaluate the performance of BM2 under varying conditions and to judge how well the model replicates the behaviour of natural systems, the nutrient forcing files for BM2 were scaled so that the new values matched the area-corrected inputs (from Monbet 1992) for three other bays from around the world (Figure 2.3). The geometry and hydrodynamics remained unchanged, but the levels of inflowing nutrient were altered in an attempt to capture the state of other bays. In an effort to produce a generic system rather than one tied to specific circumstances, the parameter set used in

Table 2.2: The recruitment relationships available in BM2. The number of recruits added to box j at time t is represented by b_{tj}. Note that the number of recruits produced by the Beverton Holt recruitment relationship is calculated at the beginning of the recruitment period, but is delivered evenly across the recruitment period rather than being delivered in a single pulse on the first day.

Recruitment Regime	Formulation	Definition of Specific Terms
Standard	$b_{tj} = J_t$	J_t = element t of the recruitment vector (constant spatially and temporally)
Beverton-Holt stock-recruit relationship (distributed evenly across the recruitment period)	$b_{tj} = \frac{\left(\frac{\alpha \cdot L_{tj}}{\beta + L_{tj}}\right)}{t_x}$	α = Beverton-Holt α for the fish group β = Beverton-Holt β for the fish group L_{tj} = biomass of larvae in box j at time t* t_x = total length of recruit period
Proportional to Primary Production	$b_{tj} = \frac{\eta_{FX} \cdot CHL_{j,t}}{\eta_{chl}}$	η_{FX} = recruitment coefficient for fish group FX $CHL_{j,t}$ = water column chlorophyll in box j at time t η_{chl} = reference level of chlorophyll (1.5)
Lognormal distribution	$b_{tj} = \frac{\lambda_{FX}}{y \cdot \sigma \cdot \sqrt{2 \cdot \pi}} e^{\left(\frac{-(\log y - \mu)^2}{2 \cdot \sigma^2}\right)}$	λ_{FX} = recruitment multiplier for fish group FX $y \sim U(0,1)$ $\sigma = 0.3$ $\mu = -0.5$ $\pi = 3.141592654$

* See equation B.11 in Appendix C.

Figure 2.3: Map of the world showing the bays used to evaluate the performance of Bay Model 2 (BM2). Symbols mark the locations of all the systems for which marine biomass or production estimates are available for comparison with the output of BM2. The bays marked with a black symbol are the bays used to set the alternative nutrient load scenarios for BM2.



BM2 with baseline ecosystem conditions is not parameterised to match the species composition of any particular bay. Instead the parameters used are based on species from temperate bays across the globe and so there is no retuning with each change in nutrient loading. This approach is also used with IGBEM (chapter 1) and proved to be robust. A range of measures, including levels of chlorophyll a (chl a), DIN, biomasses and system indices, are used to judge the model performance against available data across the entire set of bays shown in Figure 2.3.

2.4 Results and discussion

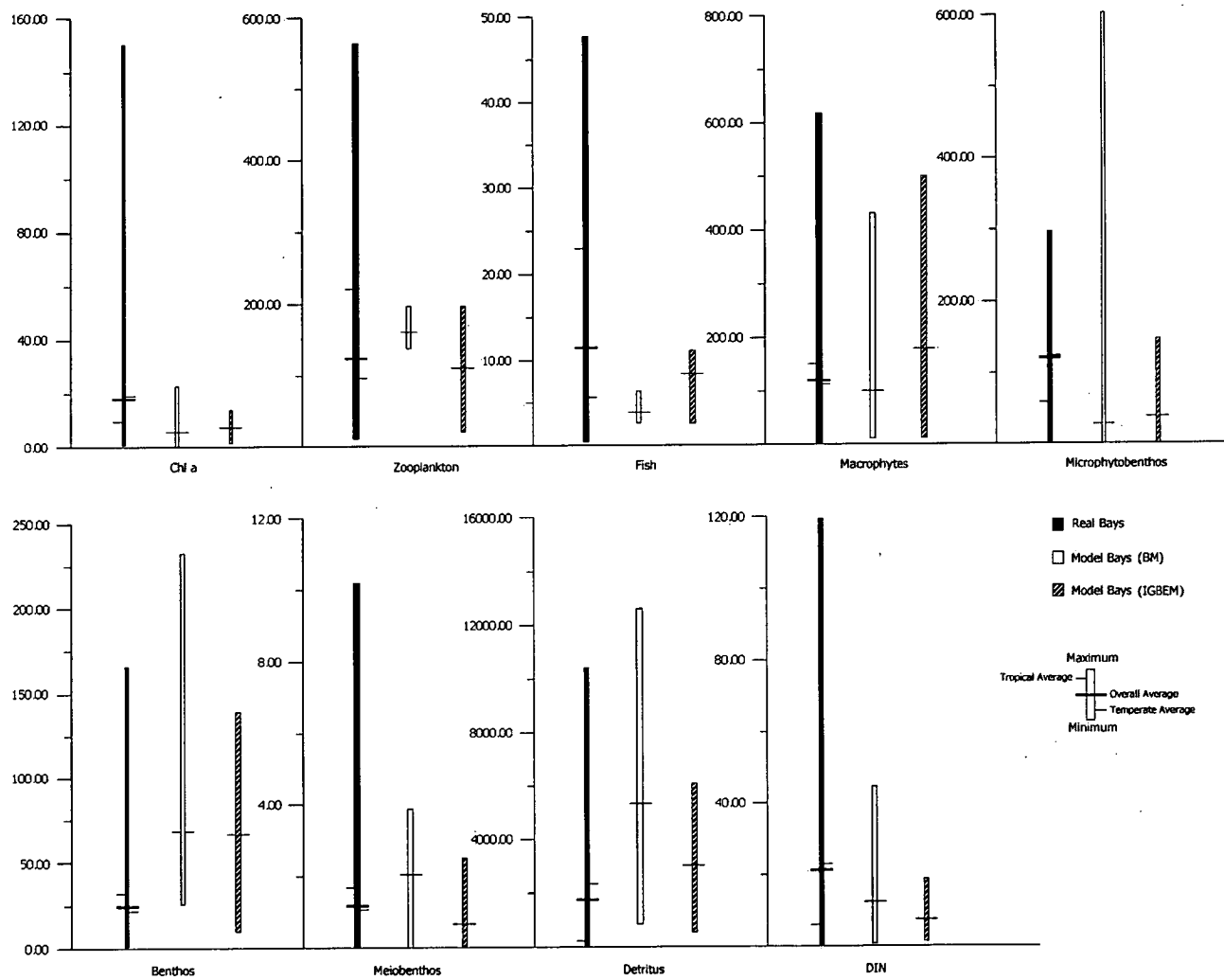
2.4.A BM2 *vs* IGBEM and real bays

The groups in BM2 and IGBEM are identical and both use the same spatial resolution and track the nitrogen content of the biomass pool, but aggregation of model output is necessary for comparison with data from real bays, which is not available at the same resolution. The pooling and nomenclature adopted during the analysis of IGBEM (chapter 1) is adopted here. The pooled outputs refer to the trophic sets: chlorophyll a (chl a) (as a proxy for total phytoplankton), zooplankton, fish, macrophytes, microphytobenthos, meiobenthos, benthos (all the other benthic consumer groups) and detritus (labile and refractory).

Range in biomass

Comparison of the range in biomass (for each trophic set) in real bays with that predicted by the models indicates that BM2 performs satisfactorily (Figure 2.4). For the majority of trophic sets the range of values produced by BM2 under different levels of nutrient forcing is within the range of empirical values from bays around the world. However, some trophic sets deviate from real world values. Ranges for the water column trophic sets for BM2 are all much smaller than their real world counterparts, whereas those for many of the benthic groups are as large (or larger) than those seen in

Figure 2.4: Range and average value for each of the main trophic sets of BM2 compared with values from empirical observations and from the output of IGBEM. The y-axis for zooplankton is biomass in mg AFDW m^{-3}; for fish, macrophytes, benthos, meiobenthos and detritus the y-axis is biomass in g AFDW m^{-2}; the y-axis for chl a is mg chl a m^{-3}; for DIN it is mmol DIN m^{-3}; and for microphytobenthos it is mg chl a m^{-2}. The values from the empirical observations are taken from Appendix A.



the field. With respect to the ranges for biomass produced by IGBEM, the ranges generated by BM2 are comparable, though they do tend to be larger. The small range of values from the models for water column variables is not surprising given the very small range of nutrient inputs used to force the models. The simulations covered the cases from baseline loadings up to x30, whereas some real systems may reach as high as x1000 (e.g. Loire Estuary in France, Monbet 1992). Trying the model under the same range of loads as seen in nature is not possible, as sufficient biological and physical forcing data is only available for systems with loads up to x30. In contrast to the water column trophic sets, the predicted ranges of biomass for the benthic trophic sets often match or exceed the empirical ranges of biomass for these sets. Therefore, the ranges for biomass predicted for the models if loading were set to x1000 are unlikely to match those observed in reality unless the benthic groups in the model experience down turns when the nutrient forcing is raised above x30. There is some suggestion of this in the model dynamics with increasing nutrients, but further evaluations at higher nutrient loads would be necessary to confirm that the pattern of declines persists as nutrient loading reach extreme levels.

That so many of the trophic sets in BM2 have a wider range of values than in IGBEM suggests that the simpler process formulation used in BM2 is not as limiting as the use of explicit physiological formulations and internal nutrient ratios in IGBEM. This may explain why the biomass ranges for the benthic groups in BM2 tend to be large. The simple assimilation equations used in BM2 apparently lack the degree of potential regulation captured in the use of internal nutrient ratios in IGBEM.

Equations of the form used for the invertebrate groups in BM2 are commonly used in water quality modelling. The field of water quality (and plankton) modelling is well developed (e.g Fransz et al. (1991) identified 20 plankton models developed since the 1970s for the Atlantic Ocean and adjoining seas) and so the equations used have

been examined extensively and their limitations and associated remedies (e.g. model closure using quadratic mortality, see Steele and Henderson 1992, Edwards and Brindley 1999, Murray and Parslow 1999b, Edwards and Yool 2000) are well understood. By comparison, ecological modelling of benthic communities is at an early stage. In particular, processes controlling the food web based on detritus are rather unclear. Therefore, the general form of the pelagic invertebrate groups is also used for the benthic invertebrates in BM2, with the addition of space based limitation of sedentary epifauna and oxygen related constraints on the infauna. This structure is adopted because there is no available information indicating that many additional processes were necessary. However, our results suggest that benthic groups and processes may be more constrained than previously thought. Detailed tracking of flows in BM2 indicates that the dynamics of the benthic deposit feeder group is the primary cause of the large biomass ranges produced for benthic trophic sets. This suggests that this group may require some form of space limitation (via a crowding effect), similar to that applied to the benthic suspension (filter) feeders. Given that these animals are largely confined to the aerobic layers of the sediment (Barnes 1987, Webber and Thurman 1991), which is typically shallow, there is a sound biological basis for this idea. Overall, results for the ranges in biomass suggest that the water column components of BM2 function well, but that the benthic components can be refined further (see chapter 3).

Average biomass

Average values of the biomass for each trophic set and the values produced under specific conditions are also informative in assessing model performance. Accounting for the magnitude of the range in the field values, the average values produced by BM2 are similar to those reported by IGBEM and observed empirically in

temperate bays (Figure 2.4). In all, 6 of the 9 trophic sets in BM2 were within 10% of the average empirical value for temperate bays and all were within 33%. The best match is by the macrophytes where the average biomass produced by BM2 is within 2% of the average of empirical observations. The worst fit is the microphytobenthos, where the difference between the model and empirical average is 32.5%. This performance is similar to that of IGBEM. More importantly, the performance of IGBEM is not consistently superior to that of BM2. Considering the 9 trophic sets in Figure 2.4, and using the average biomass as the performance measure, both models did equally well for chl a and benthic groups; the predictions of IGBEM are marginally better than BM2 for zooplankton, meiobenthos, detritus and microphytobenthos; while the performance of BM2 surpasses that of IGBEM for the fish, macrophytes and DIN. This lends further support to the view that the formulation of the water column components in BM2 is largely sufficient to capture their dynamics faithfully, while the sediment groups may require further attention if they are to behave as well as those in IGBEM.

The results for zooplankton (Figure 2.4) indicate a need for improvement of this component. The results for average biomass of zooplankton given by BM2 are restricted to the upper end of those given by IGBEM. While acceptable in a generic situation as a heuristic tool, it suggests caution in prognostic application of BM2 to natural systems (see chapter 3).

Standard relationships

Monbet (1992), Schwinghamer (1981) and Sheldon et al. (1972) identified strong system-level relationships (ecological and physical) that hold for systems from around the world. Any ecosystem model, particularly one used as a foundation model for an investigation of model structure and behaviour, should produce output that conforms to these relationships. BM2 meets this requirement.

Two of the most significant biological relationships uncovered in marine systems are the size-spectra (or "Sheldon spectra") identified by Sheldon et al. (1972) for the pelagos, and Schwinghamer (1981) for the benthos. The Sheldon spectrum for pelagic life is essentially flat (Sheldon et al. 1972), while the corresponding spectrum for the benthos is W-shaped (Schwinghamer 1981). The classes identified by Schwinghamer are pooled to match the size resolution used in the models, which converts the benthic size-spectrum from a "W" into a "U". The spectra calculated for BM2 match well with those of Sheldon et al. (1972) and Schwinghamer (1981), while those for IGBEM do not (Table 2.3 and 2.4). This is especially true for the microscopic classes, particularly in the benthos (Table 2.4). The behaviour of these classes are a major weakness of IGBEM, but not of BM2. Values for benthic classes from BM2 are well within the confidence intervals given by Schwinghamer for his general spectrum (Schwinghamer 1981).

Table 2.3: A summary of the Sheldon spectra for the pelagic classes in the run of Bay Model 2 (BM2) and the Integrated Generic Bay Ecosystem Model (IGBEM) where the environmental conditions match those in Port Phillip Bay. Following the convention set by Schwinghamer (1981) the unit area biomasses are given in cm^3/m^2.

Class	BM2 (cm^3/m^2)	IGBEM (cm^3/m^2)
Bacteria	3.48	40.50
Phytoplankton	8.72	10.02
Zooplankton	16.26	10.47
Planktivorous fish	8.84	5.45
Other (larger) fish	8.85	6.37

Table 2.4: A summary of the pooled Sheldon spectra for the benthic classes in the run of Bay Model 2 (BM2) and the Integrated Generic Bay Ecosystem Model (IGBEM) where the environmental conditions match those in Port Phillip Bay. The values given by Schwinghamer (1981) are included for comparison.

Class	BM2 (cm^3/m^2)	IGBEM (cm^3/m^2)	Schwinghamer (cm^3/m^2)
Bacteria	24.9	0.2	80.1
Meiobenthos and Microphytobenthos	5.63	0.7	6.1
Macrofauna	208.7	149.5	473.0

Monbet (1992) found a strong positive linear relationship between the logarithms of the water column concentrations of chl a (mg m^{-3}) and DIN (mmol m^{-3}). Tidal range is also an important part of this relationship as macrotidal and microtidal (>2m and <2m tidal range respectively) systems cluster separately, with little overlap (Port Phillip Bay is microtidal). Both BM2 and IGBEM comply with Monbet's relationship (Figure 2.5), but the performance of IGBEM is better than that of BM2 in which the response of chl a to DIN is flatter.

A final general relationship is that the maximum average biomass of meiobenthos decreases as the depth of the overlying water column increases (chapter 1). The biomass of meiobenthos given by the models reflects this relationship well (Figure 2.6), although those of BM2 tend to sit closer to the upper bound.

2.4.B Spatio-temporal structure and the effects of environmental change

Temporal and spatial behaviour are also important indicators of model performance. The spatio-temporal dynamics of BM2 and IGBEM are similar, and can produce sophisticated behaviours (such as competitive exclusion and long period cycles) and reproduce spatial zonation and events observed in Port Phillip Bay (PPB).

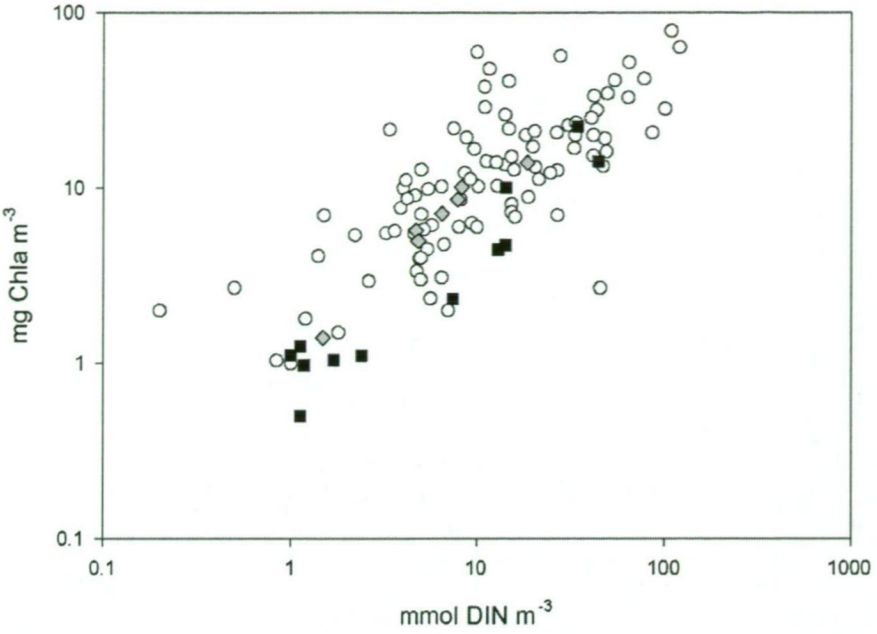


Figure 2.5: Comparison of the mean annual Dissolved Inorganic Nitrogen (DIN) against mean annual chlorophyll a (chl a) for real (open circles) microtidal marine systems (based on Monbet (1992) and additional values from the literature - see Appendix A), BM2 (black squares) and IGBEM (grey diamonds).

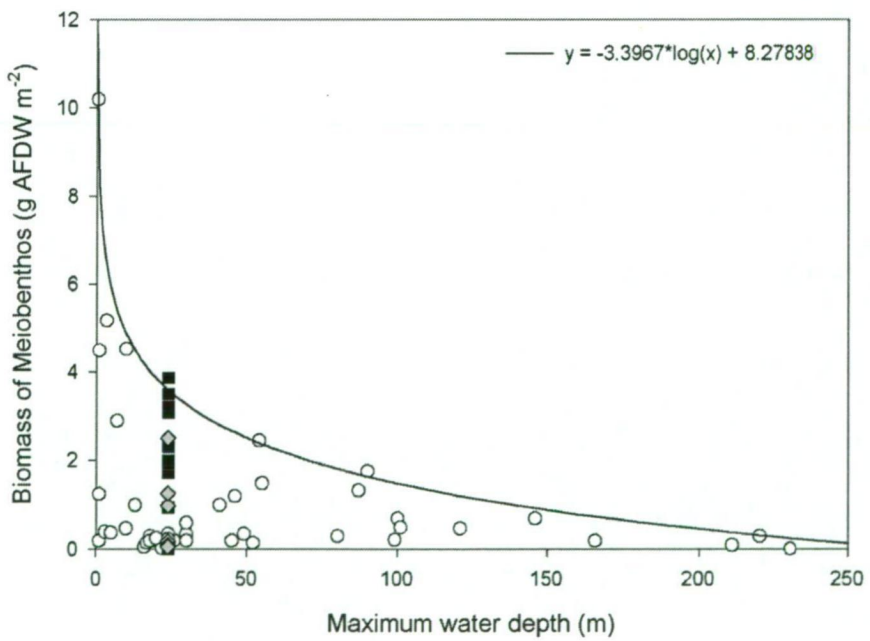


Figure 2.6: Plot of the average biomass of meiobenthos against maximum depth of the system for marine systems from around the globe (open circles), BM2 (black squares) and IGBEM (grey diamonds). The curve marking the upper bound was found by fitting the curve to the highest points in the plot (chapter 1), where y is the biomass of meiobenthos and x is the maximum water depth.

Spatial structure

The runs using the baseline nutrient loadings for Port Phillip Bay and Chesapeake Bay are designated PM and CM respectively. The predicted average biomasses per box over the final four years of the CM and PM runs, using both BM2 and IGBEM, were analysed to determine whether there are boxes that had similar biological and physical properties, which would suggest spatial patterns in the model output. The average biomasses of all groups in each box were compared on a two-dimensional non-metric Multidimensional Scaling (MDS) plot derived from a Bray Curtis similarity matrix to identify groups of boxes of similar community structure. The average values of the physical variables and the biomass per group were then examined (using the SIMPER routine of the Primer software package) to ascertain which groups determined the clustering seen. This analysis identified "areas" (boxes in the model sharing biological and physical characteristics) in the model output. Only the PM and CM runs are analysed in this way because they encapsulate the general form and dynamics of the "mesotrophic" and "eutrophic" states of the models under the current geometry and forcing.

The two models contained a similar number of areas which are located in similar positions around the bay (Figures 2.7 and 2.8). Areas predicted to share communities (dominant biological groups) were pooled to produce "zones" and, as with the "areas", the two models showed a good deal of agreement (Figure 2.9). A number of factors produced this zonation and habitat suitability alone does not explain the sharp distinction between the community assemblages around the edge of the bay and those of the central zones of the bay. In the models, these discontinuities are due to predator-prey dynamics (suppression and supply), resource partitioning and competitive exclusion, particularly in the benthos. These sophisticated behaviours are emergent in the models. An important predator-prey interaction is that of the benthic grazers and macrophytes.

Figure 2.7: Maps of the biological and physical areas (boxes with similar characteristics and community compositions) identified by the MDS, cluster and correlation analyses of the runs using the loadings for Port Phillip Bay (the PM run) of BM2 and IGBEM. Areas with the same numbers or letters within each map were part of the same cluster in the output of the analysis. (a) biological areas identified for BM2, (b) physical areas identified for BM2, (c) biological areas identified for IGBEM, and (d) physical areas identified for IGBEM.

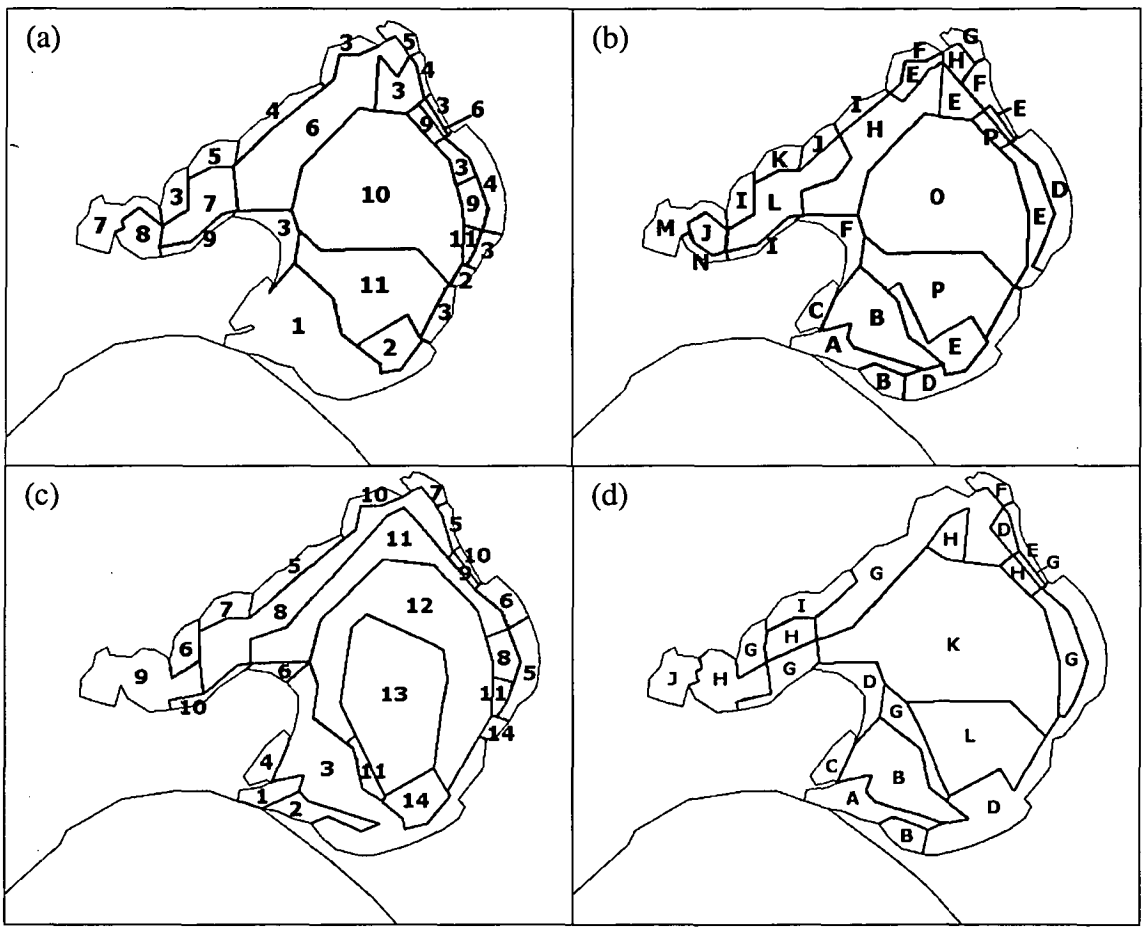


Figure 2.8: Maps of the biological and physical areas (boxes with similar characteristics and community compositions) identified by the MDS, cluster and correlation analyses of the runs using the loadings for Chesapeake Bay (the CM run) of BM2 and IGBEM. Areas with the same numbers or letters within each map were part of the same cluster in the output of the analysis and do not correspond to any of the numbers or letters in Figure 2.7. (a) biological areas identified for BM2, (b) physical areas identified for BM2, (c) biological areas identified for IGBEM, and (d) physical areas identified for IGBEM.

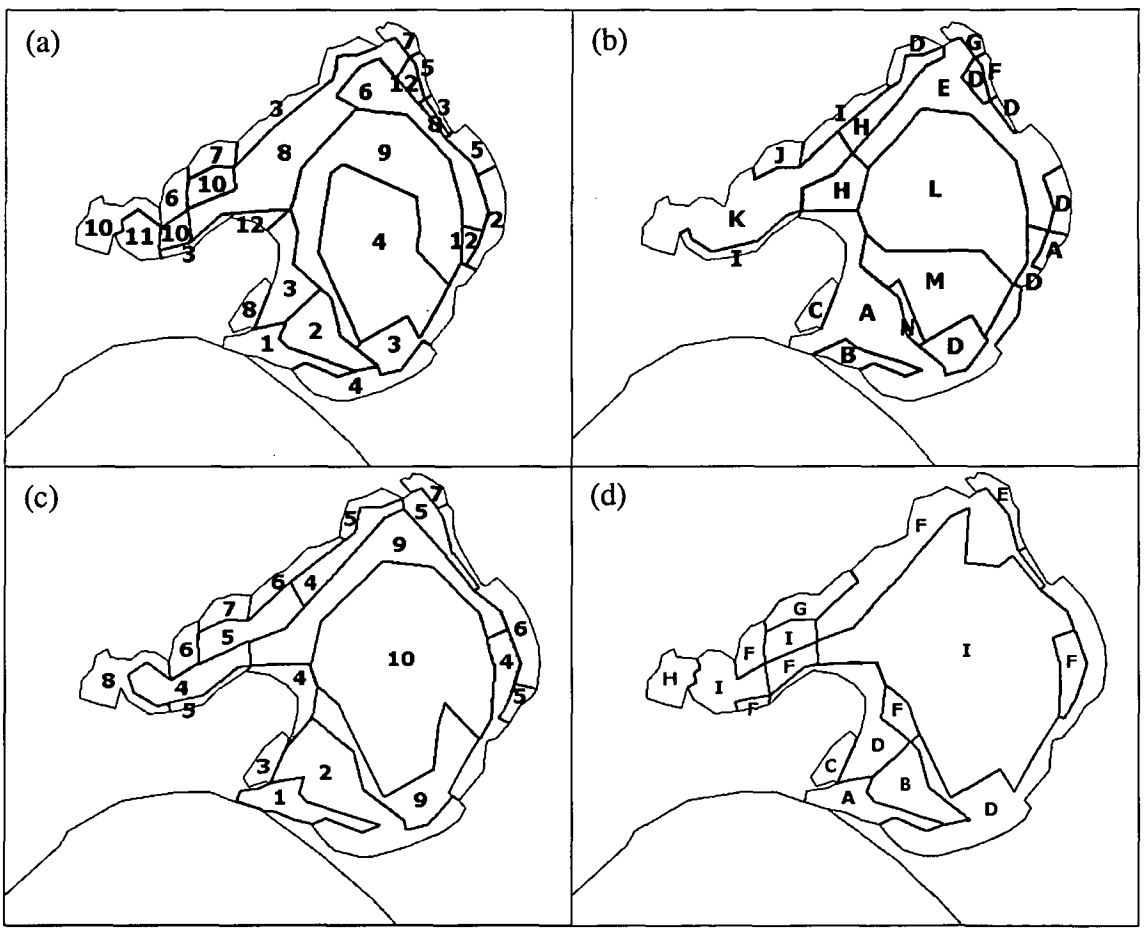
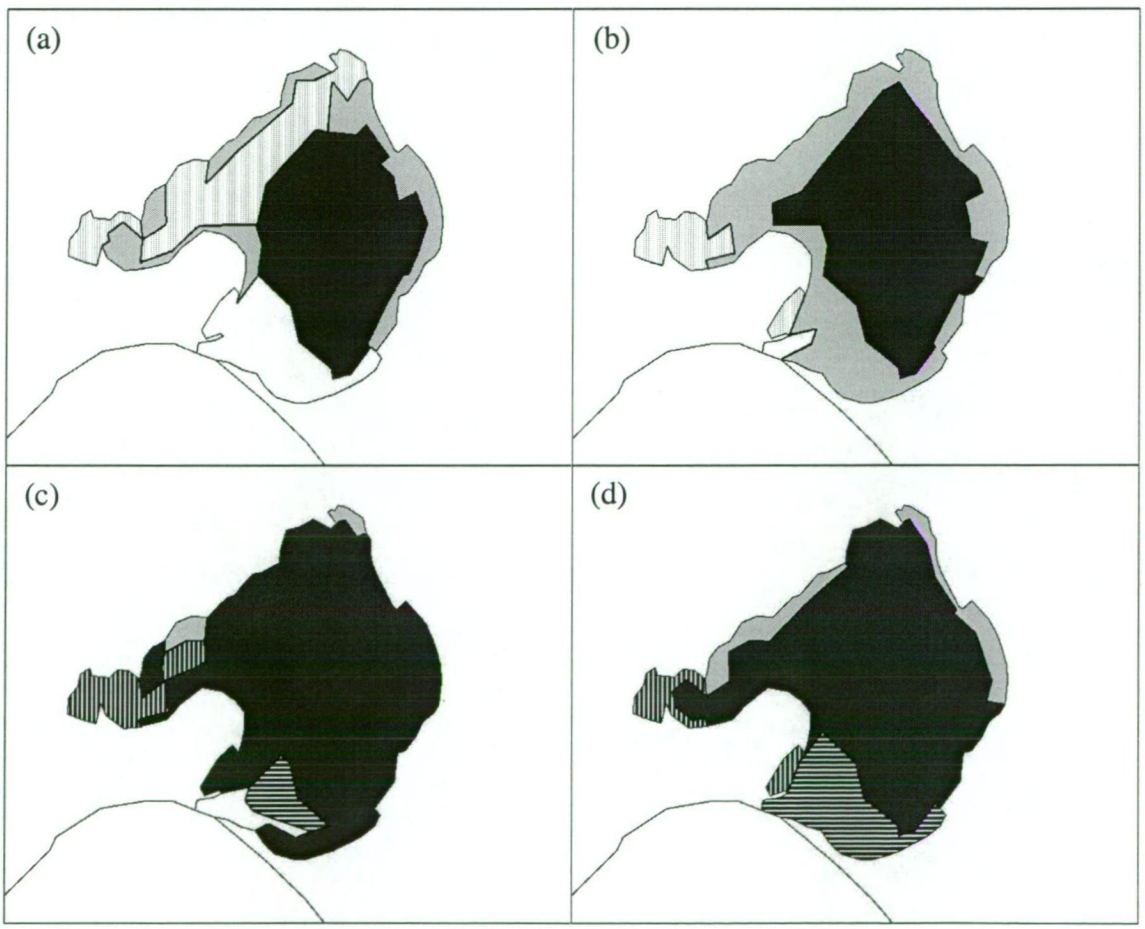


Figure 2.9: Distribution of the main zones identified in the output of Bay Model 2 (BM2) and the Integrated Generic Bay Ecosystem Model (IGBEM) (a) PM run of BM2, (b) PM run of IGBEM, (c) CM run of BM2, and (d) CM run of IGBEM. The zones in white are part of Bass Strait or heavily influenced by it; the light grey zones are characterised by specific plankton assemblages (dominated by diatoms or microplankton), as well as a rich assemblages of fish, macrophyte and benthic macrofauna; while the dark zones are characterised by another plankton assemblage (dominated by flagellates and large zooplankton), and well developed populations of meiobenthos, microphytobenthos, and bacteria.



Benthic grazers at high densities are only found in areas with persistent macrophyte populations. Further, the "macrophyte-barrens" cycle involving these groups (detailed below in the section on temporal dynamics) does not occur simultaneously around the edge but is sequential and driven, in part, by the total flows around the bay. This indicates that there is a refuge (macrophytes escape grazing) and pursuit (benthic grazers find new prey reserves) dynamic in action.

The clearest example of resource partitioning observed in the output of the models is within the detrital feeders and the effect is pronounced in BM2. The distribution of the meiobenthos and deposit feeders in BM2 show little spatial overlap and maintain healthy populations by spatial partitioning of their demands on shared food groups. If this spatial segregation is prevented by running the model on a coarser geometry (say 1 box instead of 59) then the model undergoes self-simplification and either the deposit feeder or meiobenthic group is lost (chapter 4). Usually it is the meiobenthos that goes extinct because it is both a competitor and prey of the deposit feeders. This result emphasises the importance of spatial context and differentiation in the model, as it provides a mosaic of spatial refuges and allows for emergent dynamics.

Competitive exclusion also arises in the benthic primary producer subweb, in which the macrophytes displace the microphytobenthos. The macrophytes potentially suffer from space limitation (if their biomass rises too high) and the effects of their physical environment (macrophytes are uprooted in rough conditions and epiphytes foul seagrass when nutrient levels are high). However, these factors arise only occasionally so that the macrophyte-microphyte interaction is largely driven by limiting nutrients. Because the microphytobenthos is limited by silica (Si), while the macrophytes are not, this allows the macrophytes to dominate the microphytobenthos when silica levels are low. However, the low light requirements of the microphytobenthos ensure its survival, though in reduced amounts, in the central parts of the bay where the light conditions do

not allow macrophyte growth.

Temporal dynamics

BM2 displayed many of the temporal dynamics previously reported for IGBEM (chapter 1). Both models demonstrate seasonal bloom dynamics, interannual variation and the long-term "macrophyte-barren" dynamics. However, in BM2 the interannual variation is often damped in the epibenthos, particularly in the macrozoobenthos, which shows little interannual variation. Similarly the "macrophyte-barrens" cycle is also different in BM2 compared with IGBEM. This cycle did not occur in all boxes populated by macrophytes in BM2, but arose only in the more marginal macrophyte habitats. Populations in more favourable sites showed only interannual fluctuations related to the hydrodynamic forcing and nutrient inputs. Moreover, where a "macrophyte-barren" cycle did occur it tended to have a shorter period and smaller amplitude than in IGBEM. A "macrophyte-barren" cycle has not been observed in PPB, so the dynamics predicted by BM2 appear to be closer to the natural state of PPB.

The much richer dynamics of the microfauna in BM2 translated into a wide range of temporal dynamics. These groups displayed cycles in the short, medium and long term (Figure 2.10). The short-term patterns reflected seasonal changes in growth and the availability of food. The medium term cycles gave a clear indication of the impact of the hydrodynamic forcing, which acts in the same way as reported for IGBEM (chapter 1) and PPBIM (Murray and Parslow 1997). The long-term dynamics were not as regular as the short and medium term patterns. Instead they often represented transient events (although these could last for a decade or more), after which the group would return to biomass levels and cycle characteristics very similar to those before the event (one such event is included in Figure 2.10). These "events" were caused by the coincidental occurrence of conducive physical and biological conditions

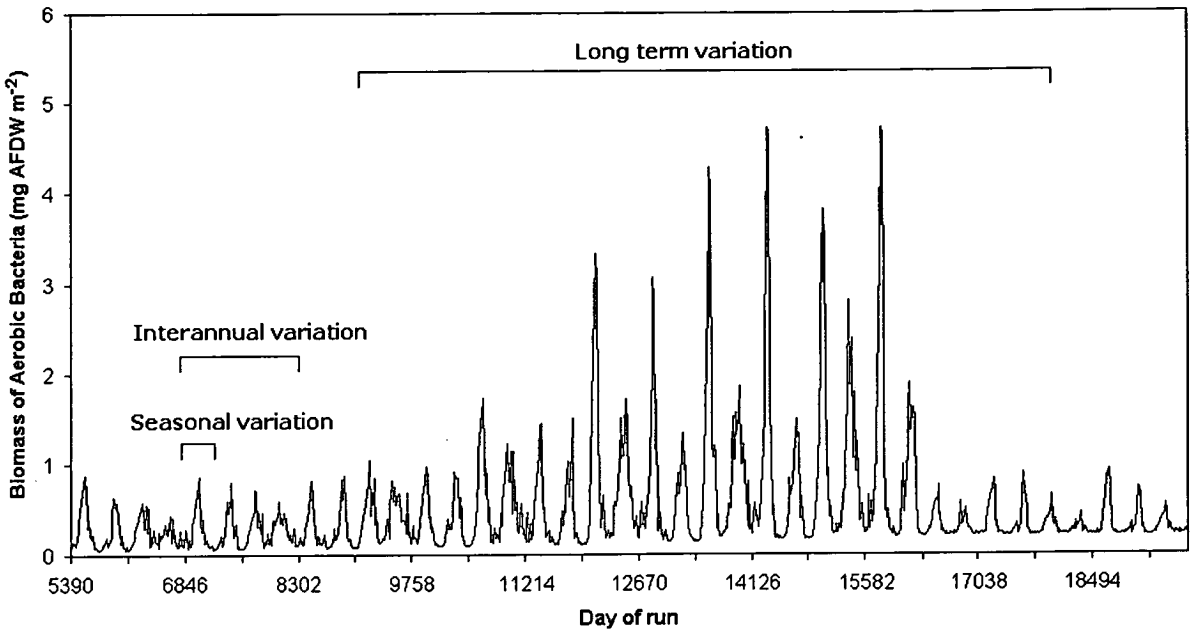


Figure 2.10: The biomass (mg AFDW m^{-2}) through time for the aerobic bacteria in box 23 (see Figure 2.1) of BM2. This time-series of biomass reveals examples of seasonal, interannual and long-term variation.

(primarily the densities of predators, prey and competitors). That both models suggest that physical and biological interactions, free from the impacts of escalating human activities, can cause substantial changes in biomass which persist for a decade or more is intriguing. It also suggests that current efforts, focused by concern over climatic change and other human impacts, may not be completely successful in separating natural dynamics and anthropogenically driven change.

Effects of eutrophication

While models can highlight that not all major changes in ecosystem structure and function are necessarily due to human intervention, they can also be instructive in showing where to look for human induced change. To be useful in identifying critical human-induced ecosystem behaviours, ecosystem models must be able to capture the gross changes that occur when a system becomes eutrophied. Both BM2 and IGBEM (chapter 1) capture the major system changes that occur with eutrophication; i.e.

simplification in biological structure, changes in relative community composition, a "left-shift" to smaller animals in the size-spectrum and an eventual drop in productivity.

BM2 (like IGBEM) predicts that, with an increase in nutrients, the communities usually found in the deep central parts of the bay expand to displace the communities typically found in shallower water along the edge of the bay (compare Figure 2.9). This in turn causes the decline of some groups (such as the benthic grazers) and the effective extinction of seagrass. Thus, the dynamics of BM2 reflect the simplification in habitat and biological diversity observed in real systems following eutrophication (Gray 1992). The only macrofaunal groups to increase are deposit feeders, which are tracked by benthic infaunal carnivores, as the levels of detritus in the sediments increase. This is symptomatic of the general habitat change that accompanies replacement of a primary production based trophic web with a detritus based web. Notably, the initial rises in biomass and productivity predicted by BM2 under a modest rise in nutrients are completely reversed when nutrients rise by x10 or more, at which point productivity drops to between 20 to 50% of the original levels and biomass drops by more than half. This is in agreement with the results of IGBEM (chapter 1) and field monitoring studies (Harris et al. 1996).

The concordance of predicted dynamics in BM2 with those in nature is also evident for water column groups. While the gross dynamics captured by IGBEM are sound, it does not capture all of the changes in relative community composition that occur with eutrophication. For example, IGBEM does not predict the increase in large phytoplankton with increasing nutrients, but it does indicate that the large zooplankton will be replaced by smaller groups (chapter 1). In contrast, BM2 correctly captures the changes in composition of all planktonic groups (Table 2.5). With an increase in nutrient load in BM2, there is a strong increase in the relative abundance of the larger phytoplankton (diatoms and dinoflagellates) and a substantial (50%) decline in the

relative abundance of the large zooplankton. This closely follows observations in the field (Murray and Parslow 1997, Park and Marshall 2000).

Table 2.5: Relative abundance of the large and small size fractions of the phytoplankton and zooplankton communities in the runs of BM2 and IGBEM using the nutrient loadings of Port Phillip Bay (PM run) and Chesapeake Bay (CM run). Empirical values for Chesapeake Bay (CB) (Madden and Kemp 1996) and Port Phillip Bay (PPB) (Harris et al. 1996) are included for comparison.

Size fraction	PM-BM2	PM-IGBEM	PPB	CM-BM2	CM-IGBEM	CB
Large phytoplankton (> 20μm)	0.30	0.27	0.28	0.65	0.22	0.75
Small phytoplankton (0.2 – 20μm)	0.70	0.73	0.72	0.35	0.78	0.25
Large zooplankton (2 – 200μm)	0.6	0.55	0.64	0.23	0.35	0.19
Small zooplankton (0.2 – 20mm)	0.4	0.45	0.36	0.77	0.65	0.81

Neither BM2 nor IGBEM predict extensive anoxia and subsequent die off of benthic and fish fauna (as seen in places such as the Baltic), but BM2 does predict seasonal drops in oxygen levels of up to 30% (due to the breakdown of phytoplankton blooms). That this does not progress to anoxia is because the bay is well mixed. The formulations used in BM2 and IGBEM should allow for the development of anoxia in suitable physical conditions, but as yet physical geometries more conducive to the formation of anoxic conditions under high loading (e.g. a deeper or more stratified bay) have not been tested. While there is no anoxia-related collapse of the fish, BM2 does predict a decline in the average size of fish. This is most severe for herbivorous fish, which decline in size by 10% or more, which agrees with patterns recorded in the field (Tober et al. 1996). This not only leaves fish vulnerable to predation for longer, but it could significantly affect recruitment. This potential effect is masked by the constant recruitment function employed in the standard runs of BM2 and IGBEM.

There are important physical and chemical consequences of increased nutrient

load, and these are more evident in BM2 due to its improved handling of the microfauna in the sediments. There is a severe drop in denitrification efficiency, particularly in the centre of the bay, as nutrient levels rise. This is severe enough under even a moderate (fivefold) rise in nutrients that the usual route of nitrogen disposal (via denitrification) is overwhelmed and nutrients build up to sufficiently high levels that they can now only be exported by flushing. Because the flushing time for PPB is close to a year (Harris et al. 1996), and the storage capacity of the bay's sediments is immense, these conditions are not easily reversed. Thus, the detritus based, highly eutrophied state of the bay persists years after the model's nutrient input levels have been reduced below those used for the PM run. This hysteresis was also observed in PPBIM (Murray and Parslow 1999) and has not been diluted by addition of other trophic groups, or the modifications made to the sediment model (see Appendix E), during the construction of BM2.

The final observation of note reflecting the effects of eutrophication is that the change in the ratio of aerobic to anaerobic bacteria in BM2 mirrored that in IGBEM. The index fell from 3.50 to 0.38 as the nutrient inputs were increased to x30 baseline levels. This suggests that this index may be a robust indicator of system-level change.

2.4.C Strengths and weaknesses

No model can be a perfect representation of nature and so each has its relative strengths and weaknesses. The behaviour of BM2 in comparison to reality and IGBEM were used to give insight into the model's strengths and weaknesses. Aberrant or inaccurate behaviour is considered a weakness, while behaviour of a component that is close to matching reality is considered a strength (especially if it used a simpler formulation than employed in IGBEM). The weakest points in BM2 stem from its simplicity, and reduced form, and are shared by all models that make the same sets of assumptions and construction choices (such as PPBIM). Its greatest strengths also come

from its reduced form and the choices made during its development.

Nutrient limitation

The omission of limitation by phosphorus was a considered decision made early in the development of BM2. Under the conditions considered here, it is a sensible choice for bays such as Port Phillip Bay that have phosphorus in excess (Harris et al. 1996). However, this may not be true of all bay systems, such as the Bay of Seine, France (Guillaud et al. 2000)). It is sensible and straightforward to include phosphorus limitation of primary production in models of natural systems where it is known that phosphorous is limiting.

The implementation of nutrient limitation and flows in ecosystem models is made easier by the observation by Redfield et al. (1963) that the major chemical constituents (N:C:P) are maintained in a relatively constant ratio (around 16:90:1). Models such as BM2 use the external (water column) nutrient ratio to determine the effective uptake of nutrients by the primary producers, whereas models such as IGBEM use the internal (cellular) nutrient ratios to determine nutrient uptake (Baretta-Bekker et al. 1997) (also see Table 2.1). Under oligotrophic conditions the application of Redfield ratios and the use of external nutrient limitation may not work. In the case of highly oligotrophic systems, such as the Baltic Sea (Thomas et al. 1999), there is evidence that only internally based Droop-like equations (formulated following the ideas of Droop 1973, 1974) will accurately reflect the dynamics of the primary producers (Baretta-Bekker et al. 1997). The nitrogen and phosphorus of the particulate organic matter in these areas is preferentially remineralised and the resulting decline in dissolved inorganic carbon (DIC) over the growing season is much greater than predicted from a Redfield ratio conversion of the decline in nutrients (Thomas et al. 1999, Osterroht and Thomas 2000). Simulation runs completed for IGBEM and BM2 in which nutrient

inputs were 20% of those in runs using baseline ecosystem conditions match these observations. The new production predicted by IGBEM is between 1.2 and 2.5 times that given by BM2 and this agrees with the findings of Osterroht and Thomas (2000) that new production based on DIC consumption is, on average, 1.5 times that based on nitrate consumption. These findings indicate that simple nutrient uptake and growth, like that in BM2, is sufficient when nutrients are in excess. However, when nutrients are low the luxury uptake of nutrients facilitated by Droop-like equations is required if system-level behaviour is to be captured faithfully.

Recruitment and movement of fish

A theoretical shortcoming of BM2 is the implementation of recruitment, movement and mortality in the fish groups. Like IGBEM, the standard runs of BM2 use constant recruitment and prescribed fish movement. These formulations do not reflect particularly realistic assumptions regarding underlying processes. Consideration of alternative formulations is crucial for judging the general performance of the standard form of the model.

The effects on BM2 of the use of these features, or their alternatives, were similar in BM2 and IGBEM. Constant recruitment buffers BM2 against large-scale changes in productivity and especially against the effects of substantial changes in fishing pressure (chapter 7). Of the three alternative recruitment schemes tested (Table 2.2), the Beverton-Holt is the most effective at correcting for aberrant effects of constant recruitment. This is important as recruitment has a substantial impact on the potential size, persistence and behaviour of the fish stocks. The stocks did demonstrate more dynamic responses to changes in nutrients and fishing pressure when a Beverton-Holt recruitment scheme is used. For instance, when fishing pressure is raised fivefold for all harvested groups the constant recruitment for the fish groups in the standard run

buffered each group equally well so the decline and subsequent stabilisation of the biomass occurred at about the same pace in each. However, in the run with the Beverton-Holt stock recruit curves the planktivores did not decline at the same pace. This is because the reduction in the number of their predators allowed them some measure of release so enough adults remained (in spite of heavy fishing) to keep the stock from total collapse for a few more years than is the case for the other groups of fish (Figure 2.11). The steepness of the Beverton-Holt relationships used varied from 0.78 for the planktivores to 0.92 for the demersal herbivorous fish (Table 2.6). While these steepness values are representative of those for many fish species (Francis 1992, Koopman et al. 2000), they were derived here by tuning the parameters so that the average number of recruits matched the constant recruitment case. It is possible that if the Beverton-Holt stock recruit curve for each group had been taken from real fish, rather than just fitted, that the steepness values may have been much lower (there are cases where steepness is as low as 0.32 (Koopman et al. 2000)). If this were the case, then the effect of using this form of recruitment may have lead to a different outcome.

Table 2.6: Steepness values for the Beverton Holt stock recruit curves implemented for the fish groups.

Group	Steepness
Planktivorous Fish	0.78
Piscivorous Fish	0.81
Demersal Fish	0.79
Demersal Herbivorous Fish	0.92

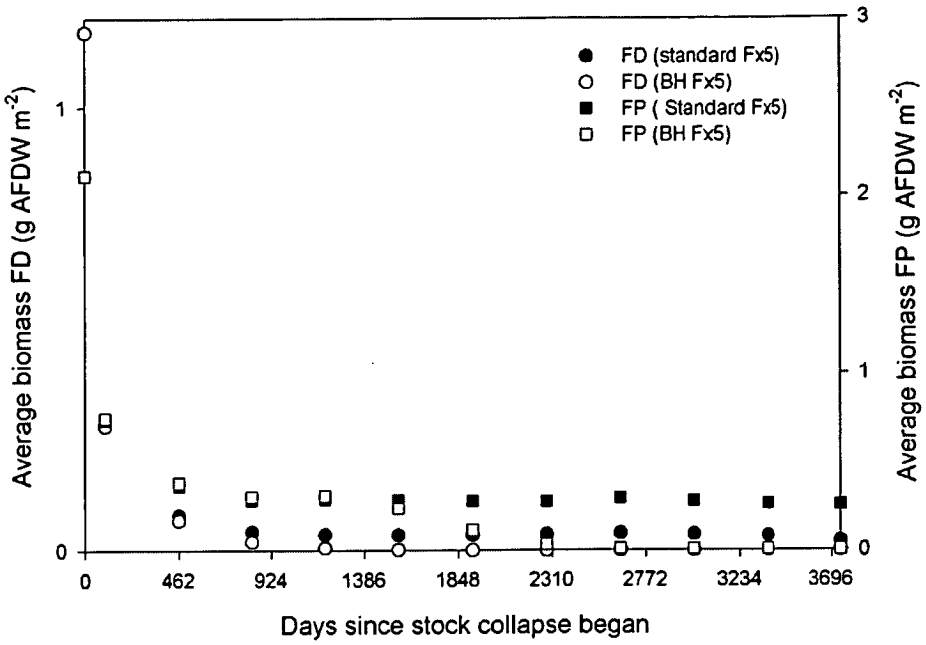


Figure 2.11: Declines in biomass of the demersal (FD) and planktivorous (FP) fish with an increase in fishing for the standard run of BM2 and the run using Beverton-Holt recruitment.

Recruitment as a function of primary production is more responsive in BM2 than in IGBEM and this is due to the greater amplitude and greater number of short period fluctuations in chl a in BM2. These fluctuations produced quite complex recruitment patterns, especially if the spawning window coincided with a spike or trough. However, the use of an index of total primary productivity as an index of recruitment is a problem in BM2, as in IGBEM, as it did not allow for a drop in recruitment with eutrophication. Use of this recruitment formulation requires the replacement of chl a (the index of total primary production used here) with a measure of abundance of a specific planktonic group as an index of year class strength.

Incorporating a random factor into recruitment, as well as density and forage dependent movement, can be used to explore broader theoretical aspects of overall model behaviour in BM2. Large recruitment and aggregation events are common in at least some harvested stocks (Samoilys and Squire 1994, Power and Atkinson 1998).

Using random recruitment or forage- and density-dependent movement to reproduce these events and consider their effects on the system as a whole could be instructive as a guide to understanding the implications of these phenomena in nature. That is not the aim of this model study though, so despite this potential they do not substantially change the existing conclusions regarding the performance of BM2.

Trophic closure

The mortality terms used for the highest trophic groups explicitly included in the model can have a substantial impact on model behaviour (Steele and Henderson 1992, Edwards and Brindley 1999). In BM2 each functional group has a linear mortality term representing the impacts of natural mortality, but ignoring the effects of higher predation. Experience with IGBEM lead to the inclusion of a quadratic mortality term for some functional groups in BM2. This quadratic term implicitly represents the effects of predation from groups not explicitly represented in the model, such as sharks, mammals and birds. Unfortunately, this did not completely correct for the problems of non-responsive higher trophic levels identified in chapter 7.

Considering the entire model food web, quadratic mortality terms are imposed on all groups that are at the edges of the web or link subwebs (such as the large zooplankton and macrozoobenthos). That is, quadratic mortality is imposed on those groups that had at least one predator not explicitly represented in the modelled web. This increased model stability and reduced the parameter space within which explosive growth is predicted, though it did not completely eradicate it across the range of parameter values that were trialled. Comparisons with IGBEM, which does not include quadratic mortality, indicates that system-level behaviours, biomasses and qualitative conclusions based on the models do not change markedly due to the inclusion of quadratic mortality. Though a more thorough sensitivity analysis may indicate

otherwise. This is a major concern within the literature discussing trophic closure in Nutrient-Phytoplankton-Zooplankton models (Steele and Henderson 1992, Edwards and Brindley 1996 and 1999, Murray and Parslow 1999b, Edwards and Yool 2000). There are problems with deducing the effects of quadratic mortality from a comparison of models built on differing premises. An investigation of the effect on model behaviour of linear and quadratic mortality on a single ecosystem model may lead to different conclusions. It was found (chapter 6) that the behaviour of BM2 with and without quadratic mortality enabled differed markedly under changing conditions and it was concluded that quadratic mortality is the most appropriate form of model closure as it allowed for realistic predictions across a range of conditions, whereas linear closure did not.

Mixotrophy

The implementation of mixotrophy in BM2 is effective as it successfully reproduced the main features of this behaviour recorded in laboratory studies. In a comparison of runs with and without mixotrophy, the biomass of dinoflagellates is increased tenfold if mixotrophy is allowed. Further, the rate of growth increased by 1.5 to 1000 times with mixotrophy and this matches the increases seen in laboratory experiments comparing phototrophic and mixotrophic growth in the dinoflagellates *Fragilidium* (Jeong et al. 1999) and *Gyrodinium galatheanum* (Li et al. 1999). This boost to growth allowed the dinoflagellates to persist when they would have dropped to negligible levels if dependent on phototropic growth alone. Thus, a weakness in many previous models is corrected by the inclusion of a rudimentary representation of a real biological process, rather than by setting growth rates to the upper bounds given in the literature (as is necessary to even partially correct the problem in IGBEM).

Attached bacteria and the sediment chemistry

The method of handling attached bacteria in BM2 also works well. It produces bacterial biomasses that match field estimates. For instance, the estimate is within 10% of that for the Kromme Estuary in South Africa (Heymans and Baird 1995), one of the few for which estimates of bacterial biomass has been made.

Even though the standard form of BM2 is a generic system rather than PPB in particular, the evaluation of the modifications made to the sediment chemistry model are best served by a comparison with the original form in the PPBIM model. The formulation used for attached bacteria in BM2 removes a weakness in the sediment chemistry of PPBIM. The original form of the empirical model used in PPBIM predicted an annual efflux from the sediments of PPB of about 11,000 to 16,000 t DIN. This is much higher than the sediment chamber estimates of Nicholson et al. (1996), which suggested the efflux is likely to be between 3,600 and 8,100 t DIN per year. The prediction by BM2 that the efflux is roughly 6,500 t of DIN per year matches this sediment chamber estimate well. Thus, the adaptation of the empirical nitrification-denitrification model of Murray and Parslow (1997, 1999) to include the dynamics of attached bacteria and infauna has preserved its strengths (such as the hysteresis discussed above), while correcting for its weaknesses.

Is less detail permissible?

The primary aim of the study presented in this chapter and chapter 3 is to evaluate whether the omission of physiological detail from an ecosystem model had a significant effect on model dynamics and the ability to represent reality. The performance of BM2 compares favourably with that of the far more detailed IGBEM. For the purposes of understanding system dynamics and at least qualitative responses to shifts in ecosystem forcing, BM2 is as capable of representing systems as accurately as

IGBEM. This shows that physiological detail is not always required and that simpler formulations, such as those employed in BM2, are generally adequate for learning and general predictive purposes. This is important because, in comparison with IGBEM, BM2 uses less than half the number of parameters, required less than one sixth of the development time, and one tenth of the time to validate, verify and calibrate.

There is some anomalous behaviour, such as the almost exponential growth of the deposit feeders under certain parameterisations and nutrient conditions (chapter 3). The occurrence of this kind of behaviour should be used to guide the application of BM2 on a site-to-site basis and under extreme conditions of change and the model may benefit from the addition of space limitation for the benthic groups (chapter 3).

2.5 Conclusions

A holistic approach to the environment is becoming an integrated part of the way resource use is thought about and dealt with (Gislason et al. 2000). As a result ecosystem models are being developed as predictive and heuristic tools. However, a lot of work remains to be done with regard to understanding the most efficient and effective ways of constructing these models. As one step in this process, BM2 was constructed to allow for an analysis of the effect of formulation detail on model behaviour and performance. Overall, BM2 does function well, reproducing patterns and values that match far more detailed models and reality. This makes it a good basis for further study of model complexity, for example, to investigate the effects of the form of grazing and mortality terms. It also indicates that it is possible to capture the qualitative dynamics of systems without resorting to highly detailed physiological structures that characterise other ecosystem models (e.g. ERSEM II (Baretta et al. 1995, Baretta-Bekker and Baretta 1997) or IGBEM (chapter 1)). This is not to say that models such as BM2 are not without drawbacks. There will be occasions when the simple formulations used in

BM2 will be incapable of reproducing the real dynamics accurately, e.g. in oligotrophic waters Droop-like equations would be needed to describe phytoplankton growth. The simpler structure used in BM2 does have some impacts on its performance in specific circumstances and this is explored in chapter 3. In many instances it would not take much effort to modify BM2 to include formulations (such as Droop-like equations) that would correct or temper these problems. Nevertheless, even without such modification and with an eye to consideration of common system dynamics and the representation of a generic temperate marine bay system, BM2 is instructive while requiring less information than other biogeochemical ecosystem models currently in use.

Chapter 3 The Effect of Physiological Detail on Ecosystem Models II: Models of Chesapeake Bay and Port Phillip Bay

Abstract

Bay Model 2 (BM2) is a biogeochemical ecosystem model. The model formulation uses general assimilation equations rather than intensive physiologically based equations to characterise the biomass dynamics of the modelled groups. The model was developed as a part of a larger study considering the effects of formulation detail on model behaviour.

The behaviour of the generic form of BM2 indicates that it can capture general system properties and behaviour (chapter 2). Consideration of its behaviour when applied to specific systems indicates that it can usually reproduce large scale patterns and levels of biomass that match those of the real system fairly well. However, its performance is not as good for some of the poorly known groups (like infauna) or when environmental conditions undergo extreme change. While BM2 requires retuning if there are very large changes in loadings on the system or when applied to new systems (a new bay), even without tuning the model is capable of predicting outcomes that are qualitatively correct. Thus, as in the generic case, the performance of BM2 is sufficiently sound to justify its use of simpler model equations (in comparison with total system models that use extremely detailed physiological equations, such as IGBEM). This supports the finding in chapter 2 that high levels of physiological detail are not always required to achieve realistic dynamics and system responses in ecosystem models, especially for the purposes of system understanding or general guidance of management decisions.

Keywords

biogeochemical, model, ecosystem, ERSEM, IGBEM, BM2

3.1 Introduction

Much of the scepticism about ecosystem models generated by the earliest such models (mainly from the International Biological Program of the early 1970s) stemmed from the fact that their complexity often saw the available resources channelled into the development and maintenance of the models not their application (Watt 1975). This failure of the IBP models to cost effectively reproduce the dynamics of the systems to which they were applied (O'Neill 1975, Patten et al. 1975, Watt 1975, Halfon 1979) lead to the belief that complex total system models failed to match reality when applied to specific systems (Silvert 1981). As a result it was decided that it was much easier, more efficient and more productive to build simpler models that dealt with fewer processes and tighter scopes (Silvert 1981). However, as ecosystem and ecological theory advance it is hard to compare results across systems if they are built on differing premises and assumptions (Halfon 1979). Consequently, large models that are flexible enough to be applied in a range of locations, and that account for a large amount of the system, are becoming attractive again. For instance, over 130 ECOPATH with ECOSIM models have been published (Christensen et al. 2000) and the European Regional Seas Ecosystem Model I and II (ERSEM I and ERSEM II) (Baretta et al. 1995) have been applied in 18 locations.

Bay Model 2 is a biogeochemical ecosystem model built as part of a wider model study considering the effects of model structure and formulation on model behaviour. As the study is concerned with considering the effects of model structure in general rather than modelling a specific bay much of the work done is set in a hypothetical generic system (e.g. chapter 2). Generic models are very useful devices for

developing theory and general system understanding, but in most circumstances models are applied to specific locations. Moreover, investigations of generic model behaviour will not necessarily answer concerns regarding applications to specific systems. Thus, a thorough evaluation of the effects of model complexity should consider model performance for specific systems as well as generic behaviours and predictions. It is this aspect of the work on the effect of formulation detail on model behaviour that is presented here. The results in a generic setting can be found in chapter 2.

3.2 Methods

Bay Model 2 (BM2) is a biogeochemical ecosystem model that uses a formulation framework based on general assimilation equations rather than intensive physiologically based equations (chapter 2). This model was compared with empirical observations from a number of real bays as well as the predicted values from another ecosystem model (the Integrated Generic Bay Ecosystem Model) run under the same environmental conditions. The Integrated Generic Bay Ecosystem Model (IGBEM) is very similar to BM2 with regard to the food web, interactions and general processes incorporated, but it includes much more explicit physiological detail. Comparing the performance of these models to each other and to empirical values from real bays should help to identify the level of detail required to capture system dynamics in specific circumstances.

The runs of BM2 considered here cover a 20 year time period and use a combination of linear and quadratic mortality, a Holling type II functional response for grazing, constant recruitment and prescribed fish movement.

The standard form of BM2 uses a spatial geometry configured for Port Phillip Bay, Australia (see Figure 2.1). Three other temperate bays (Figure 3.1) with similar physical conditions (tidal range and relative size of opening to the sea) provided a

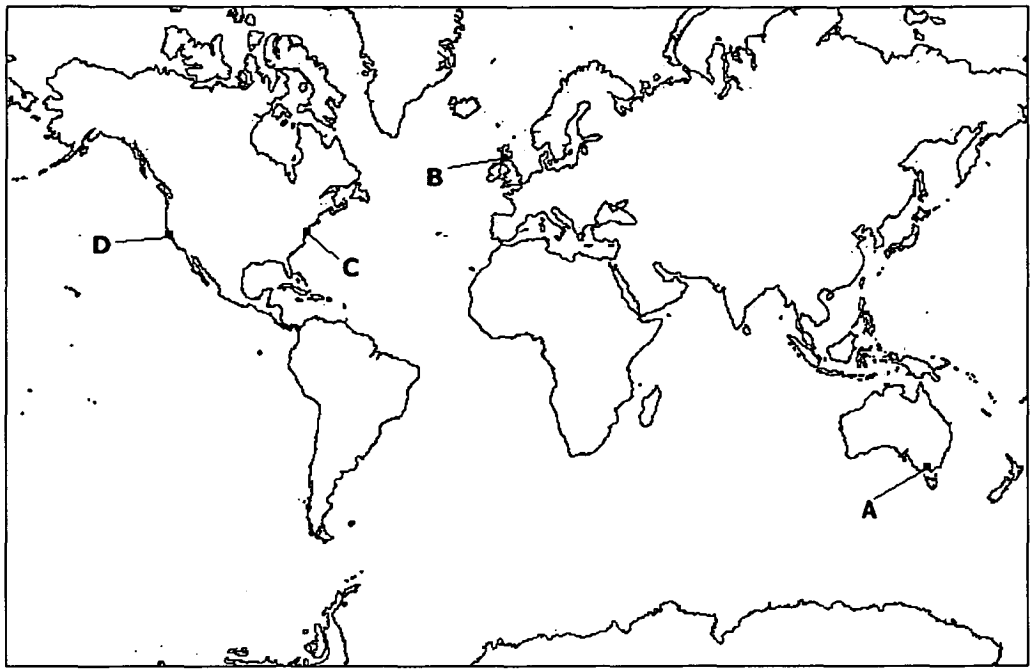


Figure 3.1: The specific bays chosen to set alternative nutrient load scenarios for BM2. A is Port Phillip Bay, B is the Firth of Clyde, C is Chesapeake Bay and D is San Francisco Bay.

foundation from which to evaluate the performance of BM2 under varying conditions and to identify how well the model replicates the behaviour of particular natural systems. Unfortunately, there is only enough available biological information to give a full assessment, comparing the entire set of values of a specific bay with those for the corresponding model, for the Chesapeake Bay and Port Phillip Bay (PPB) runs. These runs will be referred to as CM and PM respectively. The results for the other bays contribute to the findings on the generic behaviour of BM2 in chapter 2.

To reproduce the nutrient loadings in the three other bays considered, the nutrient forcing files for BM2 were scaled so that the new values matched the area-corrected inputs (from Monbet 1992) for each of the chosen bays. No attempt was made to replicate the geometry of the other bays and the hydrodynamics also remained unchanged, but the levels of inflowing nutrient were altered in an attempt to capture the state of the other bays. The biological parameters used in BM2 and IGBEM are not

changed across the various runs as there is not enough information to recalibrate to local species, or functional groups, in all cases. As the standard parameter set for BM2 is not parameterised to match the species composition of any particular bay (the parameters were based on species from temperate bays around the world), the absence of retuning for each location (i.e. with each change in nutrient loading) is justified. As part of a related piece of research (chapter 7) the parameters in BM2 and IGBEM were tuned to represent the actual species composition of PPB rather than a generic temperate fauna and flora. This work is referred to here briefly and is the only research mentioned in this paper where the standard (generic) parameter sets are not used.

The same range of measures (biomasses and system indices) and pooled trophic sets (chlorophyll a, zooplankton, fish, macrophytes, microphytobenthos, meiobenthos, benthos and detritus) that were used to judge general performance in chapter 2 were also used here to judge performance in the PM and CM runs.

3.3 Results and Discussion

3.3.A BM2 vs IGBEM and real bays

Biomasses

Comparison of empirical measures for each pooled trophic set in Port Phillip Bay and Chesapeake Bay with the predicted values of BM2 and IGBEM under corresponding nutrient load levels indicated good performance of BM2 (Table 3.1). In most cases the values predicted by BM2 are within interannual variation of the field values. However, there are some exceptions. The predicted biomass of meiobenthos is high for both the CM and PM runs (Table 3.1), but meiobenthos is difficult to sample (Schwinghamer 1981) and slight increases in the empirical estimates would see the predicted values fall within interannual variation. It is likely that a limitation term for crowding in the meiobenthos is also needed in BM2.

Table 3.1: Average value for each trophic set observed in Port Phillip Bay (PPB) and Chesapeake Bay (CB) and predicted by the associated runs (PM and CM respectively) of Bay Model 2 (BM2) and the Integrated Generic Bay Ecosystem Model (IGBEM). DIN stands for dissolved inorganic nitrogen. The values used to determine the ranges and averages for the trophic sets observed in CB and PPB are taken from Appendix A.

Set	Units	PPB	PM-BM2	PM-IGBEM	CB	CM-BM2	CM-IGBEM
Chlorophyll a	mg Chl a m^{-3}	1.04	1.00	1.40	15.85	8.95	10.10
Zooplankton	mg AFDW m^{-3}	68.47	149.17*	84.34	112.74	165.62	149.62
Fish	g AFDW m^{-2}	3.33	3.89	2.60	6.61	6.27	9.51
Macrophytes	g AFDW m^{-2}	7.75	15.19	12.52	123.60	260.84*	99.17
Microphytobenthos	mg Chl a m^{-2}	38.35	3.05*	5.13*	35.00	46.93	54.93
Benthos	g AFDW m^{-2}	29.95	45.90	32.89	80.82	85.18	82.10
Meiobenthos	g AFDW m^{-2}	0.24	1.00*	0.15	1.41	2.31*	0.84
Detritus	g AFDW m^{-2}	2953.37	3720.62	1771.96*	10417.00	7156.19*	6041.44*
DIN	mmol DIN m^{-3}	1.00	1.472	1.49	19.49	20.20	13.50

*Outside the range of interannual variation observed in the field.

The macrophyte group in the CM run is also high (Table 3.1) and this probably reflects the need to retune BM2 with substantial changes in nutrient loads. However, while this level of biomass is not representative of Chesapeake Bay, it is found in other systems with similar nutrient loading (Lotze et al. 1999). The dynamic can be traced back to the differing behaviour of phytoplankton in BM2 and IGBEM under an increase in nutrients (chapter 7). Both models include an epibenthic fouling term for seagrass, which sees seagrass decline quite sharply under high nutrients, and this in turn frees resources for other benthic primary producers. The bloom dynamics of the phytoplankton in each model then determine whether the remaining primary producers (macroalgae and microphytobenthos) exploit these resources. The phytoplankton in IGBEM produce intense blooms under increased nutrient conditions and these starve the underlying phytobenthos of light, preventing very large increases in biomass supported by the excess nutrients. In contrast, BM2 predicts only moderate blooms and these do not impede the transmission of light to the same extent as occurs in IGBEM. Consequently, light levels reaching the sediment are high enough to allow an increase in

the biomasses of macroalgae and microphytobenthos. The pattern of change and bloom dynamics predicted by IGBEM is the more common pattern in natural systems, but the pattern predicted by BM2 also arises (Conley 1999, Herbert 1999, Lotze et al. 1999).

Another symptom of the need to retune BM2 is that the dynamics of change are dissimilar under differing parameter sets. For example, with increasing nutrients the macroalgal biomass grows more than that of the microphytobenthos if the standard parameters are used, but if the parameter set employed in chapter 7 is used the situation is reversed. Although these effects are caused by the same pelagic dynamic, the final form of the effect is dependent upon the parameter set chosen.

The problems with the microphytobenthos in BM2 go beyond those already mentioned. As with IGBEM, biomasses predicted by BM2 do not match those observed in the field and they do not match the empirically observed patterns of change with increasing nutrients (Table 3.1). This may be due to the factors causing corresponding problems in IGBEM; the microphytobenthos are restricted to deeper, more inhospitable parts of the bay due to competitive exclusion by the macrophytes, and (overly efficient) infauna feeding on the microphytobenthos keeps it cropped to low levels (chapter 1). Similarly, the low levels of detritus predicted for the CM run by BM2 (Table 3.1) may reflect low input levels of detritus and overly efficient detrital feeders. The latter problem is exacerbated in BM2 as detritus feeding infauna reach higher biomasses than in IGBEM.

Potentially the most important problem with BM2 is that the predicted zooplankton biomass in the PM run is high compared to recorded values from PPB (Table 3.1). Water column modelling is well developed and usually results in very good fits to reality (Fransz et al. 1991). The failure in this case reinforces the suggestion that BM2 may require some tuning on a site-by-site basis. If it were strictly a mis-specification it could be expected that the results would be problematic for all runs, not

just those under specific nutrient loads. Regardless, when using standard parameters, BM2 tends to overestimate zooplankton biomass under low nutrient conditions. This result indicates that the standard parameter set does not work equally well over all nutrient conditions. Notably, calibrating BM2 to the dominant species in Port Phillip Bay (PPB) results in predictions much closer to values measured in PPB and to the output of IGBEM (Figure 3.2). It is likely that, unlike IGBEM which performs well across a wide range of nutrient conditions without requiring additional tuning, BM2 may require tuning to particular sites. If so, then there are important ramifications in

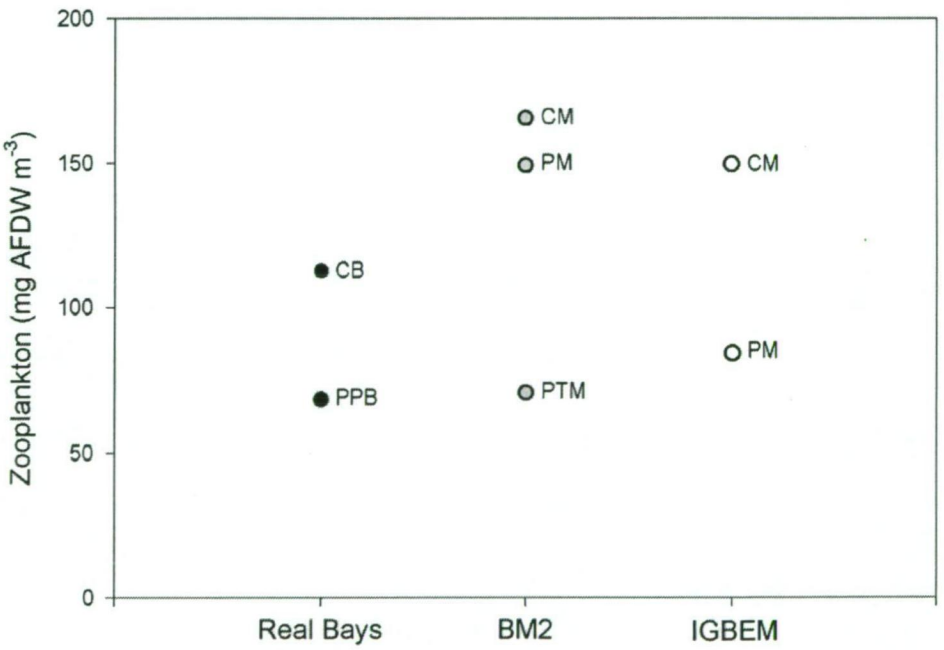


Figure 3.2: Average value for the zooplankton in Bay Model 2, in comparison with values for this trophic set in the field and in the output of the Integrated Generic Bay Ecosystem Model (IGBEM). The values used to determine the averages for the real world sets are taken from Appendix A. CB stands for Chesapeake Bay, PPB for Port Phillip Bay, PM for the model run with the nutrient loading from PPB, CM for the model run with the nutrient loading from CB, and PTM is the run of BM2 which uses a parameter set tuned to represent the biological groups of PPB rather than a standard parameter set.

applying BM2 in situations where there are large changes in nutrient loads. It was found (chapter 7) that under changing nutrient levels, there is qualitative agreement between the system-level dynamics of BM2 and those predicted by IGBEM and ECOSIM (Christensen and Pauly 1992, Walters et al. 1997). However, quantitatively there is some divergence in the models, with biomass predictions for BM2 the least sensitive to changes in nutrient loading and productivity. This implies that BM2 is capable of correctly indicating the direction of change of a system under pressure, but it may not indicate the true magnitude of this change. This failure suggests that BM2 is not as robust as IGBEM against changes in species composition, as it is more sensitive to shifts in parameter values that would probably accompany such changes in composition.

Based on the improvement in performance of BM2, relative to empirical values, when it is tuned to PPB (chapter 7), at least some of the discrepancies noted for the standard parameter set will disappear if BM2 is tuned when applied to a specific location. However, the problems identified above for microphytobenthos and meiobenthos may persist regardless of such tuning. While site-specific parameterisation of as many functional groups as possible is best, the key groups to focus on appear to be the zooplankton, zoobenthos (primarily the epifaunal carnivores) and the benthic primary producers (in particular the seagrass and microphytobenthos). The deposit feeders and meiobenthos can be sensitive to the parameter settings used, but this is more likely the result of the omission of a crucial limiting factor (e.g. the availability of space) for these groups.

Community composition

The relative composition of communities (in terms of biomass) is another informative comparison, particularly for the fish and benthic groups. This comparison is only possible for the PM run (Table 3.2) and shows that BM2 well represents patterns

Table 3.2: Comparison of the community composition for the fish and benthic groups observed in Port Phillip Bay (PPB) and predicted by BM2 and IGBEM in the runs with conditions matching those in PPB. The values given for PPB for the fish groups only include those species used to parameterise the dynamic groups explicitly included in the two models (BM2 and IGBEM).

	% of total community biomass		
Functional Group	**BM2**	**IGBEM**	**PPB**
Fish Community			
Planktivores	50.0	46.1	31.2
Piscivores	3.1	13.6	8.5
Demersal fish	41.2	36.1	50.3
Demersal herbivorous fish	5.7	4.2	10.0
Benthic Community			
Macrozoobenthos (epifaunal carnivores)	1.5	4.3	1.1
Benthic (epifaunal) grazers	11.1	4.5	4.3
Benthic suspension feeders	45.8	45.8	50.0
Infaunal carnivores	2.0	11.4	6.3
Benthic deposit feeders	39.7	34.0	38.3

of relative abundance, particularly for the benthic groups.

Estimates of the fish community produced by the models indicate that the predictions of both models are reasonably close to the values from PPB and that neither model consistently out performs the other in this area. The estimates produced for BM2 are closer to the PPB values for the demersal fish groups, but the IGBEM estimates are closer for the pelagic groups. Results for the benthic groups reflect favourably on BM2. The predicted community composition reflects that observed in PPB and BM2 performs as well as or better than IGBEM for the majority of benthic groups. Despite minor divergences, our results show that BM2 captures the large-scale community level dynamics of the fish and benthic groups.

Production and Consumption

Levels of daily production and consumption can be informative for management and scientific purposes. Reasonably accurate predictions of these values by models not only indicate their usefulness for prognostic purposes, but are also a good indication of

whether the model represents the system in a faithful manner.

The majority of the production/biomass (P/B) and consumption/biomass (Q/B) values given by BM2 are reasonably close to the empirical estimate for PPB (Table 3.3). The only two values that are less than half the PPB estimates are the P/B ratios for planktivorous fish and macrophytes. Overall, both models perform equally well. In some cases the predictions given by both models are very close (such as those for zooplankton), while in others one or the other is much closer to the PPB estimate.

Table 3.3: Comparison of the estimates of the ratios of production:biomass and consumption:biomass for Port Phillip Bay (PPB) and the BM2 and IGBEM runs with conditions matching those in PPB.

	Production:Biomass			**Consumption:Biomass**		
Set	**PPB**	**BM2**	**IGBEM**	**PPB**	**BM2**	**IGBEM**
Phytoplankton	210.3	200.1	241.8	-	-	-
Zooplankton	2.1	1.7	1.8	3.4	2.7	2.9
Fish	3.1	1.9	4.0	21.7	30.0	13.5
Planktivorous	6.3	2.1	3.2	82.6	49.8	22.4
Piscivorous	2.0	3.6	2.6	8.2	11.0	5.9
Demersal	1.5	1.4	2.1	7.1	9.9	5.7
Demersal Herbivorous	1.2	1.9	3.1	9.6	12.1	7.0
Benthos	14.2	7.7	17.0	49.0	46.5	44.1
Epifauna	9.9	6.7	5.3	17.3	30.2	8.7
Infauna	17.6	14.0	31.1	85.1	68.4	86.6
Macrophytes	22.6	8.5	12.4	-	-	-
Microphytobenthos	6.3	5.1	5.2	-	-	-

The most notable P/B values (Table 3.3) are those for macrophytes. Values predicted by the models are only about a half of observed estimates. This is largely due to the formation of a "macrophyte-barrens" cycle in the models. This is a "boom-bust" cycle, of varying period, which involves the phytobenthos, demersal herbivorous fish and the benthic grazers. In chapter 2 it was found that this "macrophyte-barrens" cycle only occurs in the more marginal macrophyte habitat in BM2, whereas it is more widespread in IGBEM. This cycle will be discussed further in the section on spatial

dynamics.

System indices

Just as ecosystem models should conform to observed empirical relationships (such as size-spectra) they must also give realistic values for system-level indices. Several of these (after Christensen 1992) were used to compare BM2 to IGBEM, PPB and the maximum, minimum and average values from a range of other coastal systems from around the world (Table 3.4). Both models generally produce realistic values for the various indices. Though both models predict a total throughput that is outside the range given by the coastal systems summarised by Christensen (1992), this probably reflects that the nutrient loads used in the CM runs are beyond those experienced by any of the bays covered by Christensen (1992).

In comparison with IGBEM, the PM run of BM2 better matches the system-level indices estimated for PPB, with the predicted value of 7 of the 11 indices close to the PPB estimates (compared with 4 for IGBEM). The match of some of the indices improves if the standard parameter set is replaced with one tuned to the species composition of PPB (from chapter 7) (for example Biomass/Throughput drops from 0.025 to 0.015, which is very close to the 0.016 estimated for PPB). However, even when tuned, the System Omnivory Index remains too low, as does the Schrodinger ratio. This is in contrast to IGBEM, where the majority of indices match once the model is tuned to represent the flora and fauna of PPB. This suggests that while the models and PPB are all quite similar in their gross form, there are internal mechanisms, linkages and other details which culminate in substantial differences in specific details (e.g. the System Omnivory Index).

Table 3.4: List of indices and their associated values for Port Phillip Bay (PPB) and the runs of the ecosystem models BM2 and IGBEM where the environmental conditions reflect those found in PPB (the PM run) or Chesapeake Bay (the CM run). The "Maximum", "Minimum" and "Averages" refer to values of these indices calculated for 8 coastal areas from around the world (from Christensen 1992).

System (or run) \ Index	Sum of flows (Throughput)	Primary Production / Biomass	Biomass / Throughput	Biomass Supported	System Omnivory Index	Dominance of Detritus	Average organism size	Path length	Residence Time	Schrodinger ratio	Relative Ascendency
Maximum	41929	74.9	0.071	0.151	0.35	0.36	0.198	5.14	0.26	52.03	36.0
Minimum	1444	3.9	0.004	0.008	0.03	0.78	0.010	2.98	0.01	2.79	21.7
Average	12204	18.9	0.026	0.057	0.19	0.57	0.083	3.70	0.10	16.76	31.1
Port Phillip Bay, Australia	13956	14.1	0.016	0.033	0.18	0.64	0.053	4.00	0.06	16.00	32.3
PM-B run (BM2 baseline nutrients)	18686	11.0	0.025	0.065	0.05	0.59	0.091	3.75	0.09	4.28	33.1
CM-B run (BM2 nutrients x10)	66216	12.9	0.021	0.048	0.05	0.60	0.077	4.04	0.09	8.03	29.2
PM-I run (IGBEM baseline nutrients)	4702	4.6	0.051	0.130	0.14	0.62	0.128	4.21	0.21	3.16	32.3
CM-I run (IGBEM nutrients x10)	50702	18.7	0.019	0.040	0.15	0.47	0.042	3.36	0.06	4.59	29.8

3.3.B Spatial structure

To consider the spatial dynamics of the PM and CM runs, the predicted average biomasses per box over the final four years of the runs were analysed to determine whether there are boxes with similar biological and physical properties. A two-dimensional non-metric Multidimensional Scaling (MDS) plot, derived from a Bray Curtis similarity matrix, was used to compare the average biomasses of all groups in each box to see whether there are groups of boxes with similar community structure. To ascertain which groups determined the clustering seen, the average values of the physical variables and the biomass per group was then evaluated using the SIMPER routine of the Primer software package. This analysis identified "areas" (boxes in the model sharing biological and physical characteristics) in the model output and any "areas" predicted to share communities (dominant biological groups) were pooled to produce "zones". The general mechanisms producing the patterns are discussed in chapter 2 and will not be repeated here; only specific details pertinent to the PM and CM runs will be mentioned.

The two models contained a similar distribution of zones around the bay in both the PM and CM runs (Figures 3.3 and 3.4). More importantly, the PM run of each model also produces a set of zones broadly similar to those identified empirically in PPB (Figure 3.3), although zonation patterns of BM2 better represent those observed in PPB than do those from IGBEM.

The communities associated with the light grey zones (Figure 3.3) are "edge" communities associated with sand and rock substrata, and they are consistently found along the edges of the bay. Communities associated with the dark grey zones in the centre of the bay are in deeper water associated with a mud substratum. The composition of these communities (Table 3.5) show some overlap (primarily in the water column groups), but there are also clear differences (especially in the epibenthos).

Figure 3.3: Spatial distribution of the main communities identified in the PM run of (a) Bay Model 2 and (b) the Integrated Generic Bay Ecosystem Model, as well as (c) those recorded in Port Phillip Bay (from findings in Hall 1992, Poore 1992, Parry et al. 1995, Beardall et all 1996, Nicholson et al. 1996, Beardall and Light 1997). Dark grey indicates a "central" community that features meiobenthos, microphytobenthos, bacteria and a discrete plankton assemblage (Table 3.5). Light grey (whether striped or solid) or white indicates an "edge" community that is usually dominated by one of two alternative plankton assemblages, along with fish, macrophytes and benthic macrofauna (Table 3.5). Note that for ease of comparison the edges of the zones for Port Phillip Bay have been matched to the boundaries of the boxes used in the models. The major landmarks of note in Port Phillip Bay are marked on (a) and the northern shore from A to B is known as the Geelong Arm.

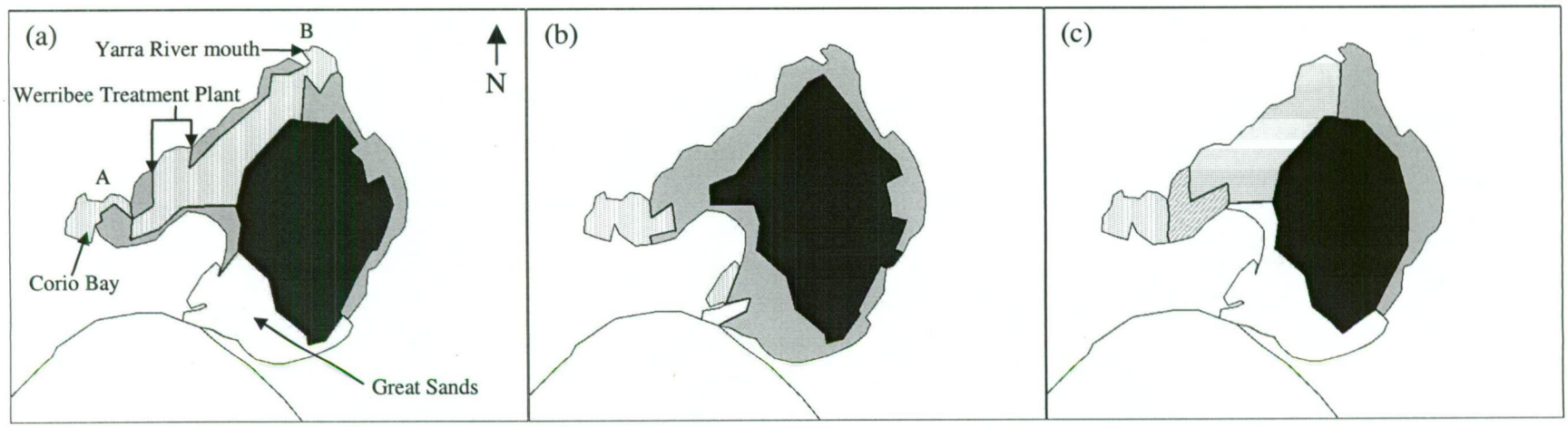


Table 3.5: Dominant groups distinguishing the "edge" and "central" communities. These groups are identified consistently in the output of both models (BM2 and IGBEM) and from field observations in Port Phillip Bay. The meaning of the codes for each of the biological groups mentioned here are given in Table 3.6. Those groups separated by an "or" indicate groups (or sets of groups) where one or the other is present at high levels, but rarely both. Remin stands for the remineralisation groups (those groups, alive and dead, associated with remineralisation).

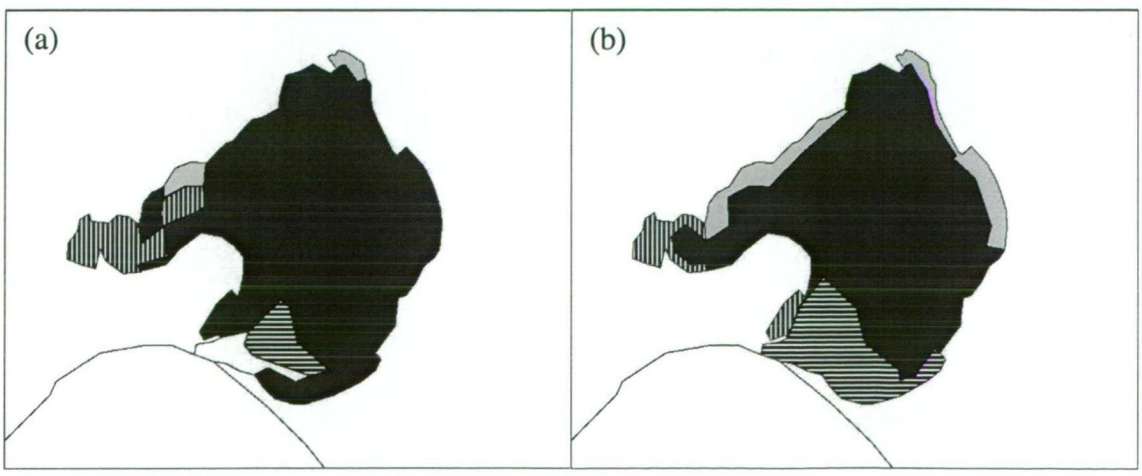
	Biological Components						Physical Characteristics
Community	**Planktonic**	**Fish**	**Epibenthic**	**Benthic**	**Macrophyte**	**Remin**	
Edge	PL, AF or PS, ZS	FP, FV, FD, FG	BF, BG, MZ	BD, BC	MA or SG	PB, DR[b], DL[b]	Moderate to high light levels, shallow to moderate depth, with high levels of bottom stress, tidal influences and DIN at some locations
Central	PS, AF, DF, HF, ZL, ZLC		BF, MZ[a]	OB, MB		AEB, ANB, DR, DL	Low light, Moderate to deep, with lower levels of DIN

a. Not predicted by IGBEM
b. Only in the Geelong Arm of the bay (Figure 3.3).

Table 3.6: Meaning of the codes used in Table 3.5.

Code	Component
PL	Diatoms
AF	Autotrophic flagellates
PS	Picophytoplankton
DF	Dinoflagellates
PB	Pelagic bacteria (attached and free living)
HF	Heterotrophic flagellates
ZS	Microzooplankton
ZL	Large omnivorous zooplankton
ZLC	Large carnivorous zooplankton
FP	Planktivorous fish
FV	Piscivorous fish
FD	Demersal fish
FG	Demersal herbivorous fish
MA	Macroalgae
SG	Seagrass
MB	Microphytobenthos
MZ	Macrozoobenthos (epifaunal carnivores)
BG	Benthic (epifaunal) grazers
BF	Benthic suspension feeders
BC	Infaunal carnivores
BD	Benthic deposit feeders
OB	Meiobenthos
AEB	Aerobic bacteria
ANB	Anaerobic bacteria
DL	Labile detritus
DR	Refractory detritus

Figure 3.4: Distribution of the main communities distinguished in the CM run of (a) Bay Model 2 and (b) the Integrated Generic Bay Ecosystem Model. Dark grey indicates a "central" community. Light grey (whether striped or solid) or white indicates an "edge" community. The characteristics of these communities are as of Figure 3.3.



The shallow to moderately deep zones along the edge of the bay are usually dominated by one of two alternative plankton assemblages, and a rich assemblage of fish, macrophyte and benthic macrofauna. In contrast, the deeper central parts of the bay are marked by a largely discrete plankton assemblage, and the macrofauna and flora typical of the bay edge have been replaced by microfauna (meiobenthos, microphytobenthos, and bacteria) which are more suited to the more stressful physical conditions found there.

There are two notable points of difference between the model and observed distributions of some groups. First, the dominance of the plankton community in the southern boxes of the models are overstated because of tidal influences, this appears to be a boundary condition artefact. This has little impact on the overall community composition and resulting zones produced by the models. The second point is that field observations (Beardall and Light, 1997) and the output of the Port Phillip Bay Integrated Model (PPBIM) created by Murray and Parslow (1997) show the highest densities of microphytobenthos along the north-west shore, from Corio Bay to the Yarra River (Figure 3.3), but reasonable levels exist throughout the bay north of the Great Sands (Figure 3.3). BM2 gives some indication of this, predicting the highest levels of microphytobenthos at points on the north-west shore, but this is patchy and the only continuous populations are in the centre of the bay. IGBEM predicts that microphytobenthos are restricted to the centre of the bay. Again, this does not have an overwhelming effect on the wider agreement between observed and predicted communities.

3.3.C Strengths and weaknesses

Regardless of the degree of sophistication, no model is an exact replica of reality. Each model has its own idiosyncrasies, strengths and weaknesses. Both the strengths and weakness present in BM2 stem from its structure and relative simplicity.

Model calibration and stability

BM2 is more sensitive to parameter settings than IGBEM and it requires more tuning on a case-by-case basis. The best example of this is the zooplankton groups (Figure 3.2). For IGBEM the values are close to the observed values, while those for BM2 require tuning if they are to closely match empirical values over a range of conditions. This characteristic was noted in PPBIM (Murray and Parslow 1997) and may be a general feature of the kind of formulation used in PPBIM and BM2.

Without site specific tuning the generic form of BM2 captures the magnitude of the system and accurately reflects the trends in community dynamics that would be caused by large-scale changes in nutrient loading. This qualitative level of information is sufficient for giving advice on management strategies and the expected effects of change, but more accurate predictions may still be desired and these can only be supplied by site specific tuning. The groups most sensitive to the parameter setting used in BM2 appear to be the zooplankton, zoobenthos (mainly the epifaunal carnivores, deposit feeders and meiobenthos) and the benthic primary producers (particularly the seagrass and microphytobenthos). Using the standard parameter values for these groups will produce spatial distributions, relative biomasses and community compositions that are close to those of the real system being modelled. However, there is a substantial improvement in biomass, production and consumption estimates given by BM2 with the site-specific tuning of these groups.

The formulation of BM2 does have implications for the stability and biological

predictions of the model. Explosive growth and associated trophic cascades are not seen in IGBEM, but they are observed occasionally in BM2, primarily in the benthic groups. In particular, the benthic deposit feeders and microphytobenthos in BM2 are observed to escape predators and undergo almost exponential growth (in turn depressing competitors and prey) under certain parameterisations and nutrient conditions. While this may be symptomatic of the sensitivity of BM2 to parameter settings, it may also imply that a critical limiting factor (such as the availability of space) has been omitted from the formulation of the benthic groups (chapter 2). As benthic modelling matures it may be pertinent to include spatial limitation, even for mobile groups and those not confined to the sediment-water interface. Alternatively, more sophisticated and dynamic grazing functions, ones that incorporate bounds or reflect the effects of predator avoidance on feeding behaviours, may produce better performance (chapter 6). In spite of these sensitivities and potential weaknesses, BM2 does capture the major changes seen in systems that are under pressure. Thus, even if only qualitatively, BM2 can give an indication of the likely consequences of a range of scenarios. Moreover, as there are fewer parameters in the model, the causes of "misbehaviour" are transparent and easily corrected.

Reduced complexity of detail is justified

Consideration of the relative performance of BM2 when applied to specific systems reinforces the conclusions drawn based on the investigation of its general dynamics (chapter 2). The output of BM2 often compares well with observations from Chesapeake Bay and Port Phillip Bay. Crucially, the performance of BM2 compares favourably with that of IGBEM under the same conditions and can even be better than it for some aspects of the system (e.g. the community composition of the benthos). However, the behaviour of BM2 is not as flexible as that of IGBEM when spanning

large changes in ecosystem forcing (e.g. large external inputs of nutrients). Moreover, BM2 occasionally produced anomalous behaviours and this should be used to guide its application on a site-by-site basis (particularly in oligotrophic conditions) and when extreme changes in ecosystem conditions are a matter of interest. Despite these warnings, for the purposes of understanding the general trends in system dynamics under current or changing conditions, BM2 is as capable of representing system behaviour as the more detailed model IGBEM. Thus it seems clear that simpler formulations are as capable of capturing the emergent properties and characteristics of marine ecosystems as larger models that include detailed physiology.

BM2 and IGBEM share many common features (like the trophic web), but they do cover a slightly different set of processes (for instance, BM2 incorporates mixotrophy while IGBEM does not). Considering their differences and their relative performances, as well as findings from the broader study of model structure on performance (this thesis) that this research was part of, there appears to be a few minimum requirements for successful system models. If a coastal ecosystem model is going to be used to aid in understanding system dynamics or predict change associated with various nutrient loads then one of the most crucial features it must include is a good representation of denitrification and sediment chemistry. This facet of the model can have a disproportionate effect on model dynamics and if handled poorly the model will not give a good indication of the effects of loading (Murray and Parslow 1997, chapter 1). More generally, ecosystem models (whether biogeochemical or not) must incorporate enough of the trophic web to capture alternative system states and community shifts associated with anthropogenic pressures, such as fishing or changing nutrient loads. This means that not only groups of interest (like harvested or indicator species) should be included, but their "supporting groups" too. These "supporting groups" often provide the links in the system which tie different habitats together (e.g.

the pelagic and demersal in shallow coastal systems) or allow for the state of the system to shift, as they have different tolerances or allow for a redirection of trophic flows when old paths are no longer efficient or available (Baretta et al. 1995, Pahl-Wostl 1997, chapter 5). The trophic web included in a model has a big impact on predictions regarding productivity, community composition and habitat structure. In one way or another these are the primary concerns of all ecosystem models. The inclusion of a good sediment chemistry model (if concerned with the effects of nutrient loads) and more importantly a food web with appropriate trophic coverage and resolution seems to be much more important than the level of detail incorporated in the formulation of these features.

3.4 Conclusions

As ecosystem approaches to resource management become increasingly common, general tools will be required and are beginning to appear (Walters et al. 1997, Sainsbury et al. 2000). Ecosystem models are becoming more widespread and some generic total system models are finding wide application (Christensen et al. 2000). As a consequence, evaluation of ecosystem models must include specific comparisons to particular systems in addition to more general analyses of performance and overall behaviour. Consideration of the biogeochemical model BM2 in this way indicated that its simpler structure was not as flexible as that of the more physiologically detailed model IGBEM. This means that while it requires more tuning on a site-to-site basis and may quantitatively break down under very large changes in nutrient loading, the qualitative predictions of BM2 do match those of other models that do not suffer any such degradation in performance with changing nutrient loads. Moreover, the model's weakness are tied to specific conditions (e.g. oligotrophic conditions), or are highlighted by anomalous behaviour (e.g. excessive benthic population expansions), or alleviated by site specific tuning and so they are easily detected, acknowledged or avoided. Thus,

despite some weaknesses, BM2 can be applied successfully to coastal marine systems and without requiring as much information as some of the other extant ecosystem models, such as ERSEM II (Baretta et al. 1995, Baretta-Bekker and Baretta 1997) or IGBEM (chapter 1).

Chapter 4 The large and the small of it: The effect of spatial resolution and sampling frequency on the performance of ecosystem models

Abstract

The effects of spatial scale on the dynamics and performance of ecosystem models is an important issue. Simplifying models by using coarser spatial resolution can be desirable, as it cuts down on computational requirements and can make model interpretation easier. Models built on simple geometries may also require relatively few data to parameterise and validate, but they may be incapable of reproducing important dynamics observed in nature. To address this issue the effect of spatial structure on the output of two trophic ecosystem models (Bay Model 2 and the Integrated Generic Bay Ecosystem Model) was considered by performing simulation runs on 1-box, 3-box, 8-box and 59-box spatial configurations. The results indicate that simpler geometries can result in less short-term variation, changes in predicted spatial patterns and trophic self-simplification (loss of functional groups), as the opportunity for spatial refuges is reduced. More importantly models with very little spatial resolution (i.e. 1- and 3-box models) do not capture the effects of eutrophication as well as do more complex models. The results for the 8-box models used here indicate that some simplification is acceptable, as overall model performance is not overwhelmed by the impacts of model self-simplification and a loss of spatial heterogeneity. However, using models with very little spatial resolution (i.e. 1- and 3-box models) can be misleading, as the impacts of the reduced heterogeneity increase.

Sampling frequency is another important issue for both empirical and model studies. Output simulating the state of the system on a daily basis was sub-sampled on weekly, fortnightly, monthly, bimonthly, half-yearly and yearly scales to evaluate the

impacts of different sampling frequencies. It is clear that sampling infrequently (> monthly) may miss important dynamics and variation, while sampling too often (< weekly) does not provide any additional benefit as useful trends are swamped by noise. An intermediate sampling frequency of between 1 – 4 weeks was sufficient to adequately represent system-level processes considered in the model.

Keywords: spatial structure, sampling frequency, biogeochemical, ecosystem, model, BM2, IGBEM

4.1 Introduction

Spatial structure and scale have been an important focus of ecology for many years (Huffaker 1958, MacArthur and Wilson 1967, Levins 1970, Maynard Smith 1974, Weins 1989, Levin 1992, Rhodes and Chesser 1996, Keitt 1997). It has been found that the scale of observations can have substantial impacts on the processes observed and how they are interpreted. For example, the generality of rocky shore intertidal communities shaped by keystone predators (Paine 1966) or competitive hierarchies (Connell 1961) on rocky shores may be reinterpreted when the influence of large-scale hydrodynamics and larval transport are considered (Roughgarden et al. 1988). Modelling studies have also found that the inclusion of the spatial dimension is important as it can allow for the production of more realistic dynamics (Sharov 1996) and prevent extinction (Nisbet and Gurney 1976, Gurney and Nisbet 1978, Keitt 1997) or competitive exclusion (Skellam 1951, Hassell et al. 1994, Johnson 1997), by providing refugia.

Regarding application of models, additional spatial resolution can require much more data for model construction, parameterisation, calibration and validation, and vast increases in computing time. These issues have often led to models being built and

applied to natural systems at point locations (e.g. Balsfjord Norway, Bax and Eliassen 1990), or the use of geometries that summarise large areas by a small number of boxes (e.g. ERSEM I, Baretta et al. 1995). While this is not necessarily a bad choice, it can be hard to discern any consequences of the use of a restricted geometry if only a single representation is employed. Studies that have included the application of the same model, or similar versions of a model (e.g. ERSEM I vs ERSEM II, Baretta et al. 1995, Baretta-Bekker and Baretta 1997), to multiple geometries can be informative. For example, Murray (2001) found that there are enough shared features between models applied on alternative spatial scales that simpler models can be used as a design tool for effective development of larger, more spatially detailed models. However, the same study emphasizes that the similarities between predictions made by the two models break down as nutrient loading changes.

The majority of research into the effects of spatial structure on the stability and behaviour of models has concentrated on relatively simple trophic assemblages (Donalson and Nisbet 1999) or substantial abstractions (Leibold 1996). Recently, international treaties and national legislation have focused attention on responsible ecosystem management, and as a result ecosystem models have become more popular. It is unclear whether findings for simpler ecological models hold for the larger ecosystem models, which have reticulated webs, mass conservation and more realistic assumptions. In an attempt to clarify this issue, two ecosystem models (Bay Model 2 and the Integrated Generic Bay Ecosystem Model) were implemented on four different geometries. This allowed for the evaluation of logistic (sampling and computational demands) and ecological impacts at the various scales.

Space is not the only dimension that causes problems in ecology and modelling. Time, and in particular how often sampling occurs, is another important topic. Sampling frequency can have a significant impact on our ability to reliably detect events and

variation over a wide range of time scales, from days to decades (Rantajärvi et al. 1998). Models can provide important insights into this issue as they present a case of perfect knowledge and can clearly demonstrate what benefits or losses are associated with particular sampling frequencies. As a complement to the consideration of spatial scale and ecosystem models, we also investigated the effect of sampling frequency on the conclusions drawn from Bay Model 2 and the Integrated Generic Bay Ecosystem Model.

4.2 Methods

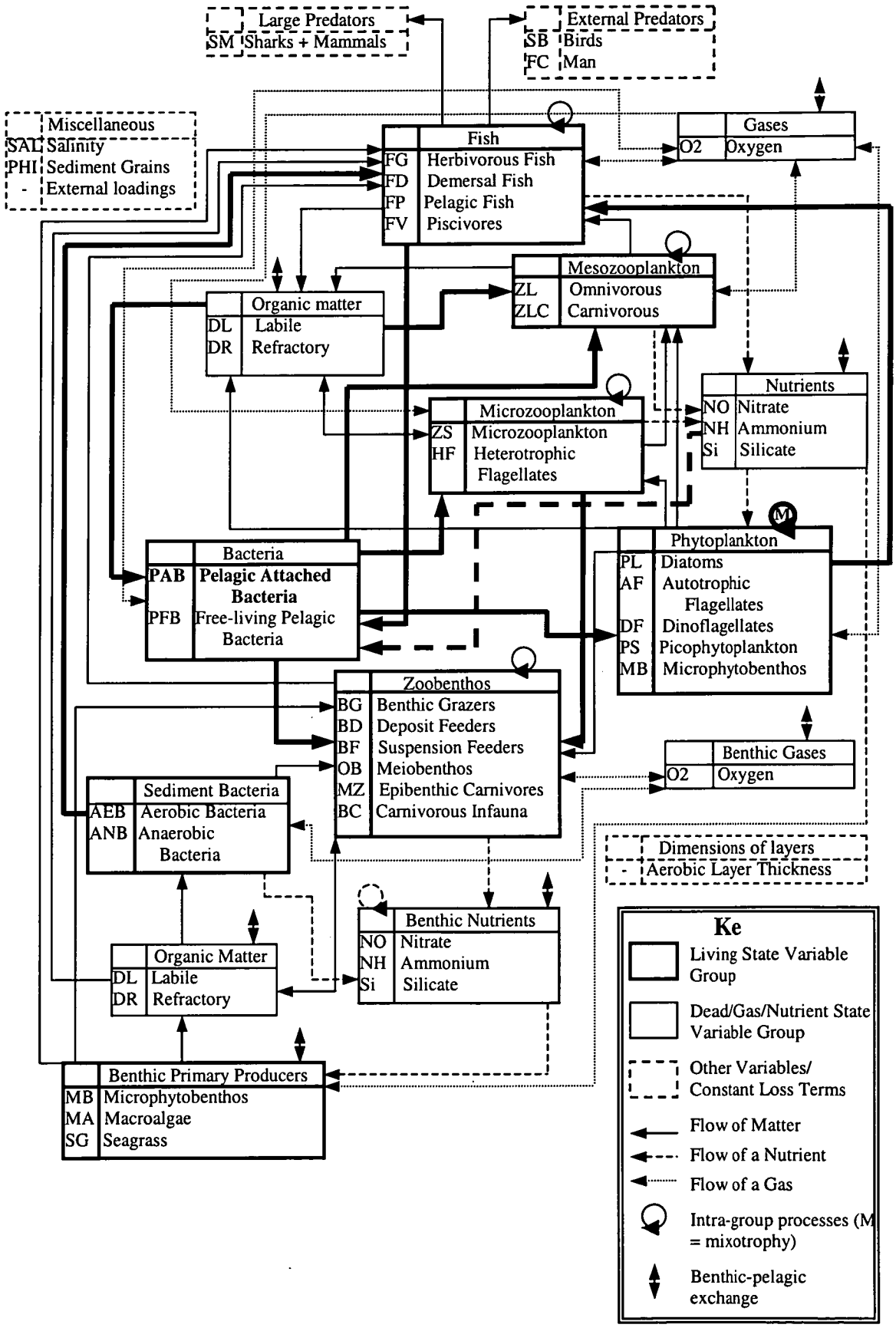
The output of two trophic ecosystem models, Bay Model 2 (BM2) and the Integrated Generic Bay ecosystem Model (IGBEM), are used to consider the effects of spatial structure and sampling frequency on model behavior and the conclusions that can be drawn from the model output. The two models were developed as a part of a wider study of the effects of model structure on performance. They cover many of the same processes and use very similar trophic webs (Figure 4.1), but the formulations used in each case differ greatly in the amount of physiological detail incorporated. A brief overview of the models follows, but a summary of the major similarities and differences between the two models is given in Table 4.1. More detailed descriptions of the formulation of the models is given in chapters 1 and 2.

IGBEM is a physiologically explicit biogeochemical process model, which follows the carbon, nitrogen, phosphorus and silicon pools of 7 primary producer groups (3 benthic, 4 planktonic), 4 zooplankton groups, 3 infaunal groups, 3 epifaunal groups and 4 fish groups (chapter 1). It was constructed from the biological groups of the European Regional Seas Ecosystem Model II (ERSEM II) (Baretta et al. 1995, Baretta-Bekker and Baretta 1997) and the physical and biogeochemical submodels of the Port Phillip Bay Integrated Model (PPBIM) (Murray and Parslow 1997, 1999a).

Table 4.1: Comparison of the underlying assumptions and formulations of the standard implementations of Bay Model 2 (BM2) and the Integrated Generic Bay Ecosystem Model (IGBEM).

Feature	BM2	IGBEM
General features		
Biomass units	mg N/m^3	mg/m^3 of C, N, P, Si
Input forcing	nutrients and physics on interannual, seasonal, tidal frequencies	nutrients and physics on interannual, seasonal, tidal frequencies
Level of group detail	functional group	functional group
Process related		
Bioturbation and bioirrigation	yes	yes
Consumption formulation	type II	mixed (type II, type III)
Formulation detail	general: only growth, mortality and excretion explicit	physiological: the processes of assimilation, basal/ activity/stress respiration, defecation, excretion, ingestion, mortality are all explicit
Light limitation	optimal irradiance fixed	phytoplankton can acclimate to ambient light levels
Mixotrophy	dinoflagellates	none
Nutrient limitation	external nutrients determine uptake	internal nutrient ratio determines nutrient uptake and disposal
Nutrient ratio	Redfield	internal specific nutrient ratio
Oxygen limitation	yes	yes
Sediment burial	no	yes
Sediment chemistry	dynamic, with sediment bacteria	empirical, sediment bacteria are a tracer only
Shading of primary producers	yes	yes
Spatial structure	flexible with the potential for multiple vertical and horizontal cells	flexible with the potential for multiple vertical and horizontal cells
Temperature dependency	yes	yes
Transport model used for hydrodynamics flows	yes	yes
Model closure		
Top predators represented by static loss terms	yes	yes
Linear mortality terms	yes	yes
Quadratic mortality terms	yes	no
Fish and fisheries related		
Age structured fish	9 age classes	9 age classes
Fishery Discards	target species only	target species only
Invertebrate fisheries	yes	no
Stock-recruit relationship	constant recruitment	constant recruitment
Stock structure	external: the reproductive stock outside the bay produces the recruits and the oldest age classes migrate out of the bay to join this stock	external: reproductive stock outside the bay produces the recruits and the oldest age classes migrate out of the bay to join this stock

Figure 4.1: Trophic webs of Bay Model 2 (BM2) and the Integrated Generic Bay Ecosystem Model (IGBEM). Flows marked in bold, and pelagic attached bacteria, are features of the web in BM2 that are not present in IGBEM.



This framework was then extended to cover benthic biological groups omitted from ERSEM II (those in the benthic primary producer subweb) (chapter 1). This level of process and trophic detail is at the upper bound of what is normally employed in ecosystem models currently in use (e.g SSEM (Sekine et al. 1991) and ERSEM II (Baretta-Bekker and Baretta 1997)) and it makes IGBEM one of the most highly detailed ecosystem models published.

BM2 was developed from PPBIM by extending the framework of that model to cover all of the groups in IGBEM. Consequently, BM2 includes the same trophic groups and physical details (vertical layering, transport, mixing and spatial geometry) as IGBEM, but there are important differences. The two models differ in the formulation of the attached bacteria (chapter 2) and dinoflagellates, but the greatest difference lies in the degree of process detail used in their formulation (Table 4.1). In BM2 physiological processes are not modelled explicitly, but are dealt with as a whole by generalised equations for assimilation and waste production (chapter 2). In addition, BM2 models only the nitrogen components and relies on Redfield ratios, rather than internal nutrient ratios, to determine the form of nutrient dependent activities. This general level of detail is more representative of most existing models of eutrophication and water column trophic dynamics (Fransz et al. 1991).

4.2.A Spatial structure

The transport model used as the physical basis of BM2 and IGBEM can be applied on any geometry (any number of boxes). The standard geometry used during development was 59 boxes (Figure 4.2a), but we also ran both ecosystem models on 8, 3 and 1-box equivalents (Figure 4.2b-d), constructed by summing over the flows between boxes. The standard configuration was used in each case (standard parameter set, 2-weekly record period, 20 year run with physical forcing files repeated every 4 years).

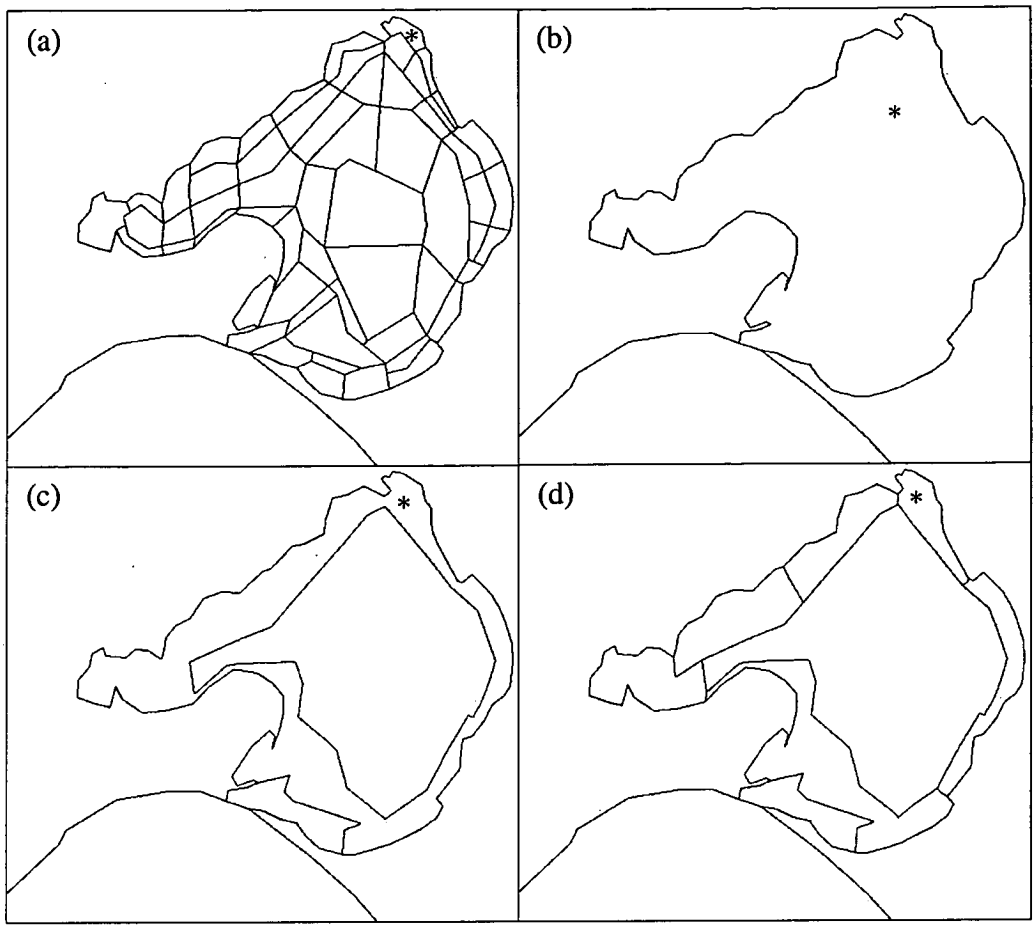


Figure 4.2: Maps of the geometries used with the models: (a) 59-boxes, (b) 1-box, (c) 3-boxes, and (d) 8-boxes. The "*" marks the box receiving inputs from the Yarra River (reference site for later figures)

However, for numerical stability, it was necessary to retune some of the groups in BM2. This is because the coarser model geometries average out the physical conditions and BM2 is sensitive to environmental conditions (chapters 2 and 3). The groups that required retuning were the metazoan infauna (meiobenthos, deposit feeders and benthic infaunal carnivores), and the planktivorous and demersal herbivorous fish.

Only the final four years of the full twenty-year simulations are used to judge the model performance as this removes the chance of confounding due to transient dynamics produced by initial conditions. Relative production, consumption and biomasses, or the variance of these measures, were found to be the most useful way of

comparing model behaviour across several geometries. To check for consistency in the results across varying environmental conditions, the runs were repeated when fishing pressure or nutrient load was increased or decreased fivefold.

4.2.B Sampling frequency

The start date, end date and sampling frequency of the output of BM2 and IGBEM is flexible. Daily output is possible, but the standard runs use fortnightly records due to storage requirements and our desire to mimic achievable intensive monitoring of natural systems. This feature was used to consider the implications of differing sampling frequencies. IGBEM and BM2 were run for 20 years under a standard configuration, except that model output was stored daily for the final 2 years of the run (storage of a longer time-series was not possible due to the immense storage requirements). This output was sub-sampled weekly, 2-weekly, monthly, 2-monthly, quarterly, half-yearly and yearly. The summary statistics of model behaviour used include the variance of production, consumption, biomass and denitrification estimates. Effects of shifting nutrient loads and fishing rates away from their baseline values were also considered by repeating the sub-sampling on runs where these forcing conditions were increased or decreased fivefold.

4.3 Results

4.3.A Spatial structure

Smoothing of local variation

Comparing the variance in the time-series for any of the groups or processes with rapid dynamics (such as chlorophyll a, zooplankton or denitrification) across the various model geometries indicates that decreased spatial resolution reduces short-term fluctuations. This effect is clearest close to point source inputs such as the Yarra River,

which flows into the northern most point of the bay (Figure 4.2). Comparing the variance in chlorophyll a (chl a), over the final 4 years of each run, in the box fed by the Yarra River there is a strong decrease in variance with increasingly aggregated geometries, regardless of the model chosen (Figure 4.3). There is also a decrease in the variance of bay-wide averages with coarser spatial resolution, but it is an order of magnitude smaller (Figure 4.4). The variance observed at the bay-wide scale is much smaller than in the box fed by the Yarra river inputs because at the bay-wide scale fluctuations across the bay cancel each other out or are subsumed by the more stable behaviour of boxes further from input sources.

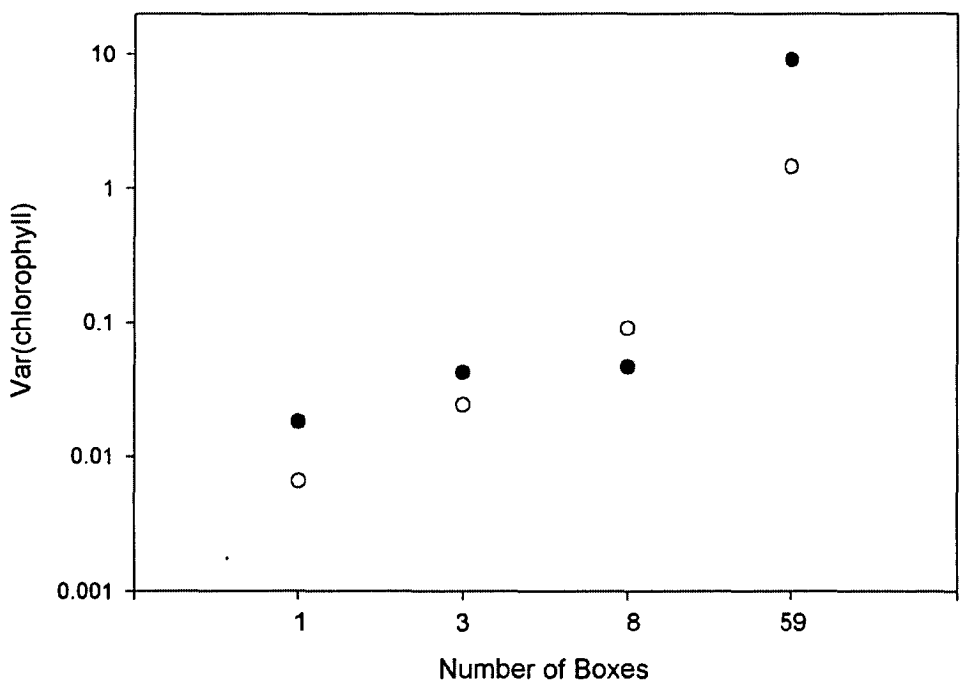


Figure 4.3: Variance of chlorophyll a in the "Yarra River" box (marked by a * in Figure 4.2) over the final 4 years of the 20 year runs for different levels of spatial resolution in the Bay Model 2 (open circles) and Integrated Generic Bay Ecosystem Model (solid black circles) models (1 – 59 boxes).

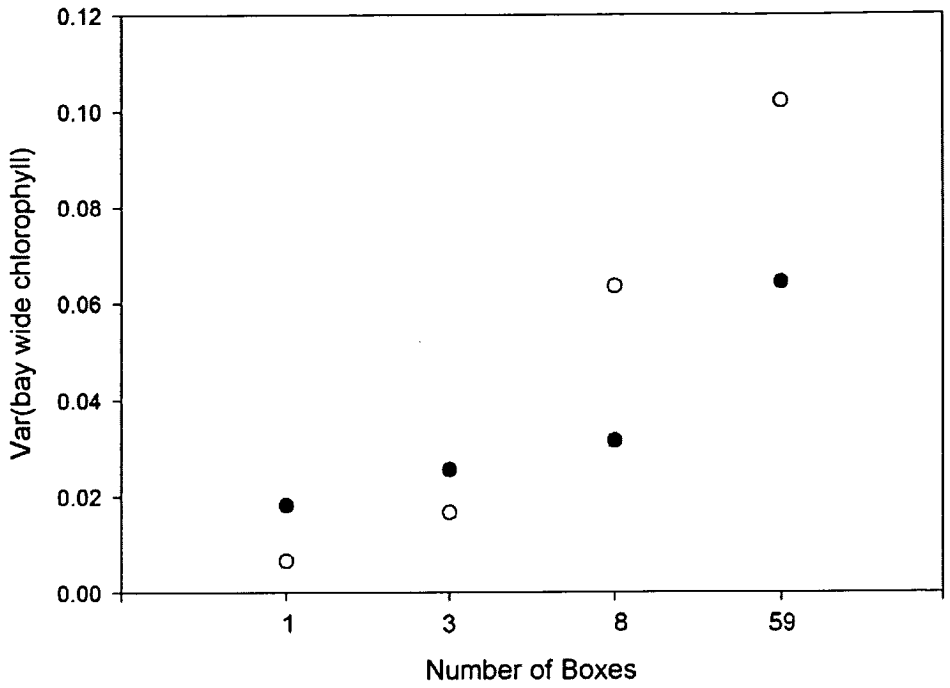


Figure 4.4: Variance in the bay-wide average chlorophyll a over the final 4 years of the 20 year run for different levels of spatial resolution in the Bay Model 2 (open circles) and Integrated Generic Bay Ecosystem Model (solid black circles) models (1 – 59 boxes).

Self Simplification

Potentially the most important effect of the use of differing geometries is that the simpler geometries may not support the same food web as the 59-box case. In both models trophic self-simplification (i.e. loss of functional groups) occurs when using the simpler geometries (Table 4.2). In the water column groups, this simplification is illustrated by the dependence on boundary conditions reseeding of the affected groups (they persist only in the southern most boxes and their patterns of change are strongly tied to the tidal forcing across the bay mouth). Within the benthos, simplification results in the effective extinction of several groups (with the biomass dropping to <0.00001% of the value in the 59-box model). In some cases the effect of reduction in spatial

Table 4.2: Persistence of the trophic groups in runs of Bay Model 2 (BM2) and the Integrated Bay Ecosystem Model (IGBEM) using 8-box, 3-box and 1-box geometries. The state of a trophic group after 20 simulated years are indicated by: Y = wide spread and as abundant as in the 59-box geometry; R = restricted in distribution compared with the 59-box geometry; BC = persists only because of continual reintroduction from the Bass Strait boundary box; D = >75% reduction in abundance; and NO = decline to baywide extinction. Note that pelagic attached bacteria are not present in IGBEM.

	BM2			IGBEM		
Trophic Group	**8-box**	**3-box**	**1-box**	**8-box**	**3-box**	**1-box**
Diatoms	Y	Y	Y	Y	Y	Y
Picophytoplankton	Y	BC	BC	D	D	D
Autotrophic flagellates	Y	Y	Y	BC	BC	BC
Dinoflagellates	BC	BC	BC	Y	Y	Y
Heterotrophic Flagellates	BC	BC	BC	BC	BC	BC
Microzooplankton	Y	Y	D	D	D	D
Large omnivorous zooplankton	Y	Y	Y	Y	Y	Y
Large carnivorous zooplankton	Y	Y	Y	Y	Y	Y
Pelagic attached bacteria	Y	Y	D	-	-	-
Pelagic free bacteria	BC	BC	BC	Y	Y	Y
Planktivorous fish	Y	D	D	Y	Y	Y
Piscivorous fish	Y	D	D	Y	D	D
Demersal fish	Y	D	D	D	D	D
Demersal herbivorous fish	Y	Y	D	Y	D	D
Microphytobenthos	BC	BC	BC	BC	BC	BC
Macroalgae	R	NO	NO	R	NO	NO
Seagrass	Y	Y	D	Y	Y	Y
Aerobic bacteria	D	D	D	D	D	D
Anaerobic bacteria	D	D	D	D	D	D
Meiobenthos	D	NO	NO	NO	NO	NO
Benthic deposit feeder	R	Y	NO	Y	Y	Y
Benthic infaunal carnivores	R	Y	NO	Y	Y	Y
Benthic filter feeders	Y	D	Y	R	Y	Y
Benthic herbivorous grazers	Y	Y	D	Y	Y	Y
Macrozoobenthos	Y	Y	Y	Y	Y	Y

structure is obvious even for the 8-box geometry, while other groups show restricted distribution in the 8-box case and only undergo bay-wide extinction in the 3-box and 1-box runs (e.g. macroalgae (Figure 4.5)).

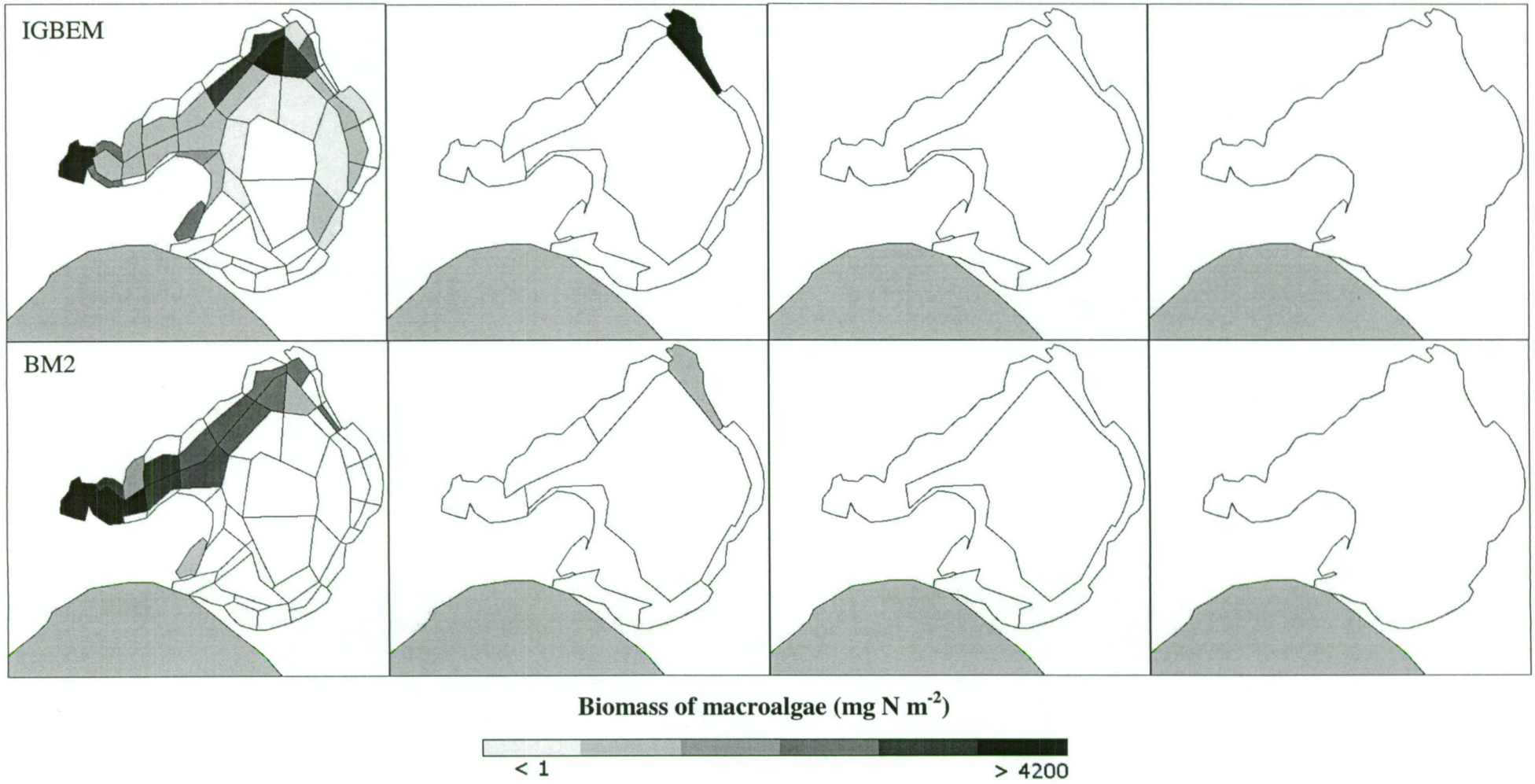
The self-simplification of the food web is not as strong across both models. IGBEM loses half as many groups as does BM2 for the same reduction in spatial resolution. The groups lost from IGBEM are also lost from BM2 except for autotrophic flagellates, which shows no reduction in abundance in BM2 irrespective of the spatial resolution employed. It is worth noting that the groups that are lost are all from the lower to mid-trophic levels and are generally either microscopic or infaunal (Table 4.2). The single exception is macroalgae, which is replaced by seagrass on the simpler geometries.

Even those groups that are not totally displaced on the coarser geometries may show depletion (Table 4.2). This is because they can no longer partition resources with competitors or escape predator coverage as easily. The geometries with coarser spatial resolution have more homogeneous physical conditions, as gradients in depth, nutrients and hydrodynamic properties are reduced or removed. The reduction in the size of these gradients affects the outcome of local interactions and partitioning of resources becomes less likely. In addition, the models use differential equations and so, without lags imposed by spatial structure, groups cannot escape the influence of their predators or competitors.

Overall estimates

Those groups that are removed or depleted by self-simplification of the food web on coarser geometries obviously do not have similar biomass estimates across all model geometries. Within the groups that do remain, several display a relatively constant average biomass across all the geometries. Large carnivorous zooplankton in

Figure 4.5: Effects of spatial resolution on self-simplification. This example shows that the distribution of macroalgae is contracted to the point of extinction with decreasing spatial resolution. The maps show the distribution of macroalgal biomass (mg N m^{-2}) on day 6594 of the run for each geometry of the Bay Model 2 (BM2) and Integrated Generic Bay Ecosystem Model (IGBEM) models.



BM2 is one example, with its mean biomass varying by less than 2% across the geometries. In contrast, others increase either as a result or cause of the depletion of other groups. For example, the biomass of autotrophic flagellates in BM2 increases by 145 - 160% in the run using 1-box compared with the run using a 59-box geometry. This increase is largely as a result of an increase in influence of the boundary conditions in the less spatially resolved geometries.

The effect of changes in biomass on higher level aggregated measures can vary from minor to substantial. For example, the bay-wide average oxygen concentrations within the sediments is almost identical regardless of the geometry used, while the average bay-wide biomass of pooled biological groups is between 1000x too low to 4x too high depending on the group of interest and which of the simpler geometries is used (Table 4.3). Notably, total benthic primary production, sediment bacteria and denitrification are too low when using fewer boxes in either model. This triplet failure is pronounced as these things are all closely linked; low levels of benthic primary production result in lower levels of detritus, which in turn means that there is less bacterial activity and lower rates of denitrification. Aside from this triplet, the performance of IGBEM was relatively consistent across all geometries, with most estimates for the coarser resolution being within a twofold range of those for the 59-box model. In contrast, the performance of BM2 shows widespread deterioration on the lower geometries, with 40% of the estimates for the coarser geometries falling outside a twofold range of the estimates from the 59-box model.

Spatial zonation

The physical characteristics of each cell are increasingly "smeared" as spatial resolution is decreased. As a consequence, there is less of a gradient in community structure and processes from the edge to the centre, and from the north to the south of

Table 4.3: Relative (value from the lower geometry run / value from the 59-box run) biomass, production and consumption for the runs of Bay Model 2 (BM2) and the Integrated Bay Ecosystem Model (IGBEM) on the smaller geometries. Any entries in bold signify a difference of more than twofold between the simpler geometry and the 59-box case.

	BM2			IGBEM		
	1-box	**3-box**	**8-box**	**1-box**	**3-box**	**8-box**
Bay-wide Average Biomass						
Chlorophyll a	1.26	1.69	1.59	1.11	1.34	1.05
Zooplankton	0.76	1.18	0.93	0.92	0.93	0.92
Fish	**0.27**	**0.44**	0.64	0.76	1.20	1.73
Benthic primary producers	**0.42**	1.29	1.04	0.77	**0.23**	0.64
Benthos	**0.02**	**2.84**	**3.56**	1.09	0.83	1.03
Infauna	**0.00**	**2.96**	**3.73**	1.09	0.83	1.03
Epifauna	**0.40**	0.69	0.55	1.02	0.80	0.78
Pelagic bacteria	1.57	0.98	1.04	0.56	0.63	0.72
Sediment bacteria	**0.09**	**0.09**	**0.33**	**0.19**	**0.23**	**0.26**
Oxygen	0.99	0.99	1.00	1.00	1.00	1.00
Bay-wide Annual Totals						
Denitrification	**0.00**	**0.00**	**0.01**	**0.02**	**0.06**	**0.13**
Water column primary production	1.03	1.30	1.01	**2.87**	1.97	0.74
Benthic primary production	**0.03**	**0.27**	**0.14**	0.54	**0.26**	**0.34**
Water column secondary production	1.56	1.53	1.08	1.22	0.90	0.81
Benthic secondary production	**0.02**	1.11	0.80	1.06	0.97	0.61
Water column consumption	1.45	1.47	1.08	1.10	0.88	0.79
Benthic consumption	**0.09**	0.79	0.94	1.11	1.08	0.64

the modelled bay. Moreover, because the cells cover larger areas as spatial resolution declines, any group that is present in cells on the smaller geometries will cover a larger part of the bay. It follows that the spatial distribution of groups that do persist on the smaller geometries can be much more widespread than in the 59-box case. The best examples of this are in the benthic groups, especially in IGBEM (Figure 4.6). As a result of wider distributions, areas of the bay are less clearly demarcated on the smaller geometries. The distinctive "edge" and "central" assemblages in the 59-box case are less clear on the 3- and 8-box geometries, as more microfaunal groups are ubiquitous, and of course any spatial zonation is impossible in the 1-box case (Table 4.4).

Figure 4.6: Effects of spatial resolution on the spatial distribution of functional groups. This example shows that the distribution of benthic deposit feeders expands with loss of spatial resolution. The maps show the distribution of the biomass (mg N m^{-3}) of benthic deposit feeders on day 7280 of the run for each geometry of the Bay Model 2 (BM2) and Integrated Generic Bay Ecosystem Model (IGBEM) models.

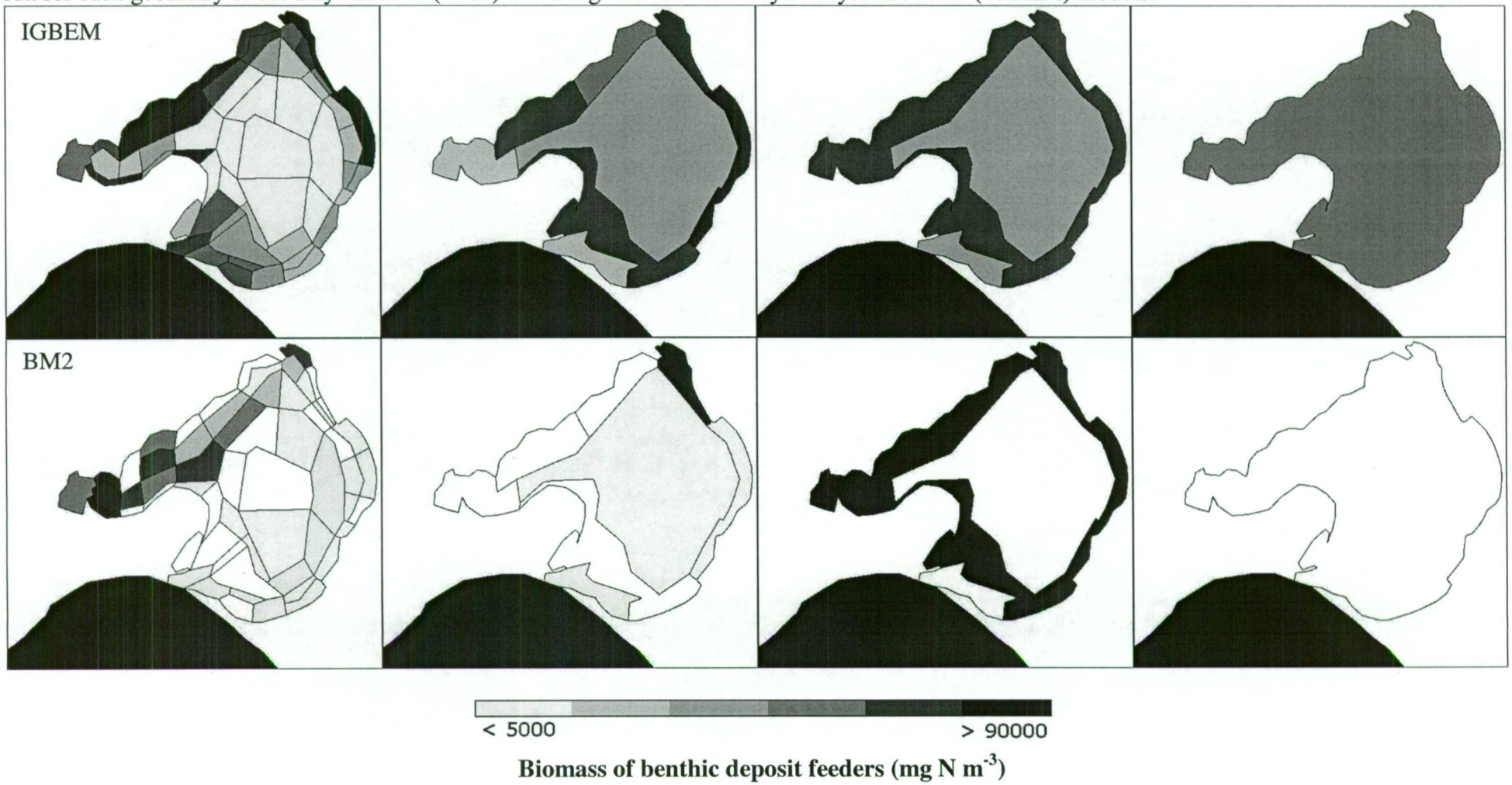
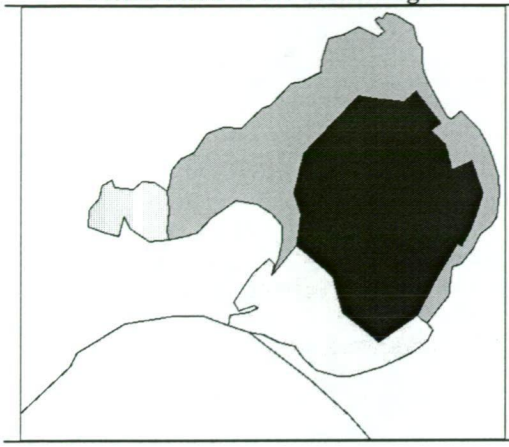
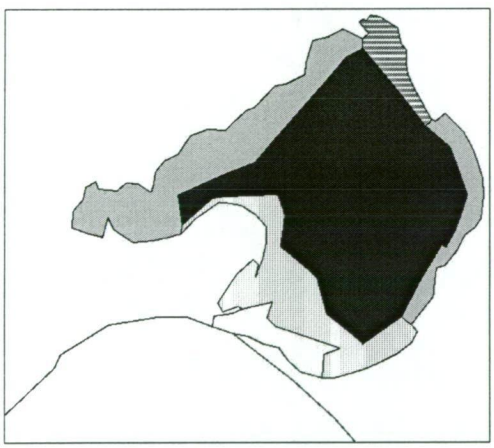
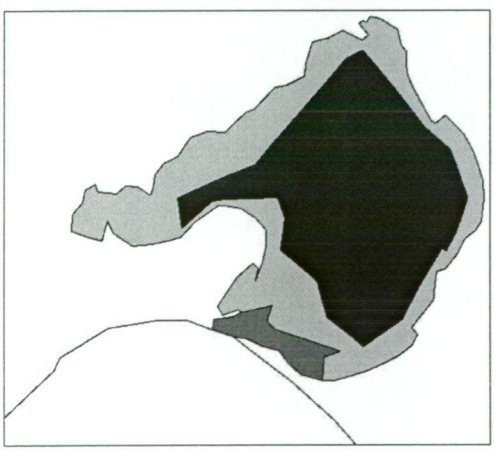


Table 4.4: Spatial distribution of assemblages predicted using Bay Model 2 (BM2) on 59-, 8- and 3-box geometries (the distributions predicted by the Integrated Generic Bay Ecosystem Model are very similar). Boxes containing the same assemblage have been grouped together and shaded in the same colour. Groups marked in bold differ from the 59-box composition.

Distribution of the assemblages	Edge Assemblage	Central Assemblage
	Diatoms and Autotrophic flagellates or Picoalgae and Microzooplankton Planktivorous fish Piscivorous fish Demersal fish Herbivorous demersal fish Benthic filter feeders Benthic herbivorous grazers Macrozoobenthos Benthic deposit feeders Benthic infaunal carnivores Macroalgae Seagrass Pelagic Bacteria	Picoalgae Autotrophic flagellates Dinoflagellates Heterotrophic flagellates Large omnivorous zooplankton Large carnivorous zooplankton Benthic filter feeders Macrozoobenthos Meiobenthos Microphytobenthos Aerobic bacteria Anaerobic bacteria Detritus
	Picoalgae, **Dinoflagellates** and **Heterotrophic flagellates** or Diatoms and Autotrophic flagellates **Large carnivorous zooplankton** Planktivorous fish Piscivorous fish Demersal fish Herbivorous demersal fish Benthic filter feeders Benthic herbivorous grazers Macrozoobenthos Benthic deposit feeders Benthic infaunal carnivores **Meiobenthos** **Microphytobenthos** Macroalgae Seagrass Pelagic Bacteria **Aerobic bacteria**	**Diatoms** Picoalgae Autotrophic flagellates Dinoflagellates Heterotrophic flagellates **Microzooplankton** Large omnivorous zooplankton Large carnivorous zooplankton Benthic filter feeders Macrozoobenthos Meiobenthos **Pelagic Bacteria** Aerobic bacteria Anaerobic bacteria Detritus
	Diatoms Autotrophic flagellates Picoalgae **Dinoflagellates** Microzooplankton **Large omnivorous zooplankton** **Large carnivorous zooplankton** Planktivorous fish Piscivorous fish Demersal fish Herbivorous demersal fish Benthic filter feeders Benthic herbivorous grazers Macrozoobenthos Benthic deposit feeders Benthic infaunal carnivores **Microphytobenthos** Seagrass Pelagic Bacteria **Detritus**	**Diatoms** Picoalgae Autotrophic flagellates Dinoflagellates **Microzooplankton** Large omnivorous zooplankton Large carnivorous zooplankton Benthic filter feeders Macrozoobenthos **Pelagic Bacteria** Aerobic bacteria Anaerobic bacteria Detritus

Model divergence with changing pressures

Self-simplification of the model food web (i.e. the loss of functional groups) and inconsistencies in predicted estimates of biomass, production and consumption also occurred with decreasing spatial resolution when nutrient loading and fishing pressures are altered (increased or decreased). However, the nature of the effect of changing spatial resolution does not always match those of the runs under baseline conditions (Tables 4.5 and 4.6). Generally, changes in nutrient loading produces corresponding changes in the resource base, particularly for the benthic groups, and this underpins effects of spatial resolution on simplification. The impacts of a reduction in spatial resolution observed under baseline conditions are expressed at a different level of spatial resolution when nutrient loads or fishing pressure is changed. If nutrients increased, the effects of self-simplification largely disappear from the 8-box case, while decreasing nutrients usually intensifies the effects of self-simplification. A reduction in nutrient load intensifies the effects of simplification for all but two groups in the 8-box version of BM2 (Table 4.5), but in IGBEM some groups show fewer effects of a reduction in spatial resolution. This may indicate that IGBEM has some sensitivity to the forcing conditions used, but that they are at a different point to, and not as strong as, those identified in BM2 (chapters 2 and 3). The effects of changing fishing pressure are not so easily characterised, beyond the observation that trophic cascades are stronger on simpler geometries. The lack of heterogeneity with coarser spatial resolution allows predators and prey to overlap for longer periods and over larger areas. Thus, cascades caused by the release or depletion of fish are more pronounced and extend further through the web on the simpler geometries.

Table 4.5: Groups demonstrating different responses to spatial structure under alternative amounts of fishing and nutrient loads in Bay Model 2. The number(s) in brackets after the group name indicates the geometries (in terms of the number of boxes used) where the effect of spatial resolution differed from runs using the baseline forcing. The meaning of the codes for the state of a trophic group after 20 simulated years are: "Macrophyte barren cycle" = longterm boom-bust cycling of macrophytes; "Constant" = only small scale interannual variation present; "More widespread" = wider spatial distribution even accounting for larger cell sizes on coarser geometries; Y = wide spread and as abundant as in the 59-box geometry under the same forcing conditions; R = restricted in distribution compared with the 59-box geometry under the same forcing conditions; BC = persists only because of continual reintroduction from the Bass Strait boundary box; D = >75% reduction in abundance; and NO = decline to baywide extinction.

Conditions	Change in response to spatial structure	Groups
Increased fishing pressure	Macrophyte barren cycle → Constant	Seagrass (8,3)
	D → BC	Microzooplankton (1)
	Y → BC	Microzooplankton (8,3)
Decreased fishing pressure	BC → D	Picoalgae (3,1)
	D → Y	Planktivorous fish (3)
	More widespread	Seagrass (8,3)
	Y → BC	Diatoms (3)
	Y → D	Picoalgae (8)
		Piscivorous fish (8)
		Demersal herbivorous fish (3)
		Benthic infaunal carnivore (3)
		Benthic filter feeder (8,1)
	Y → NO	Benthic deposit feeder (3)
Increased nutrient loading	BC → Y	Dinoflagellates (8,3,1)
	D → Y	Meiobenthos (8)
		Anaerobic bacteria (8,3)
	More widespread	Seagrass (8,3)
	R → Y	Macroalgae (8)
		Benthic deposit feeder (8)
		Benthic infaunal carnivore (8)
	Y → BC	Picoalgae (8)
	Y → R	Benthic filter feeder (8)
Decreased nutrient loading	D → Y	Meiobenthos (8)
	R → Y	Benthic deposit feeder (8)
	Y → D	Herbivorous demersal fish (3)
	Y → NO	Benthic infaunal carnivore (3)

Table 4.6: As for Table 4.5, but for the Integrated Generic Bay Ecosystem Model.

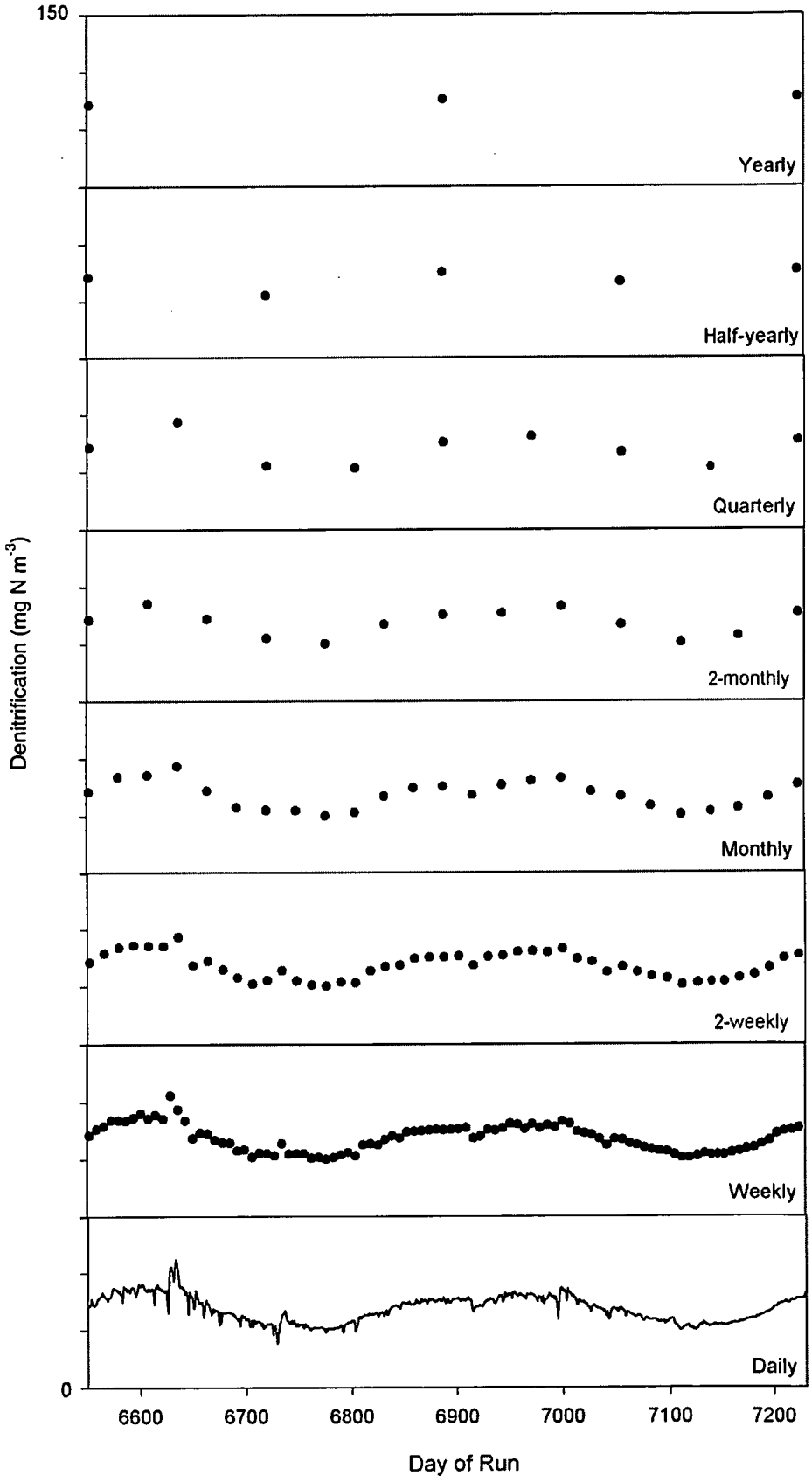
Conditions	Change in response to spatial structure	Groups
Increased fishing pressure	D → Y	Microzooplankton (8,3,1)
	More widespread	Diatoms (8,3)
		Large omnivorous zooplankton (8,3)
		Seagrass (8,3)
		Benthic deposit feeder (8,3)
		Benthic infaunal carnivore (8,3)
	R → D	Benthic filter feeders (8)
	Y → D	Planktivorous fish (3,1)
		Piscivorous fish (8)
		Demersal herbivorous fish (8)
Decreased fishing pressure	More widespread	Benthic deposit feeder (8,3)
		Benthic infaunal carnivore (8,3)
	R → D	Benthic filter feeders (8)
	R → NO	Macroalgae (8)
	Y → D	Piscivorous fish (8)
		Demersal herbivorous fish (8)
Increased nutrient loading	D → Y	Picoalgae (8)
		Microzooplankton (8)
		Demersal fish (8)
	R → NO	Macroalgae (8)
	R → Y	Benthic filter feeders (8)
	Y → D	Dinoflagellates (1)
		Large omnivorous zooplankton (3,1)
		Macrozoobenthos (8,3,1)
Decreased nutrient loading	D → Y	Picoalgae (8,3,1)
		Microzooplankton (1)
		Demersal fish (8)
		Demersal herbivorous fish (1)
		Anaerobic bacteria (8,3,1)
	More widespread	Microzooplankton (8,3)
		Benthic deposit feeder (8,3)
		Benthic infaunal carnivore (8,3)
		Macrozoobenthos (8,3)
	R → NO	Macroalgae (8)

4.3.B Sampling frequency

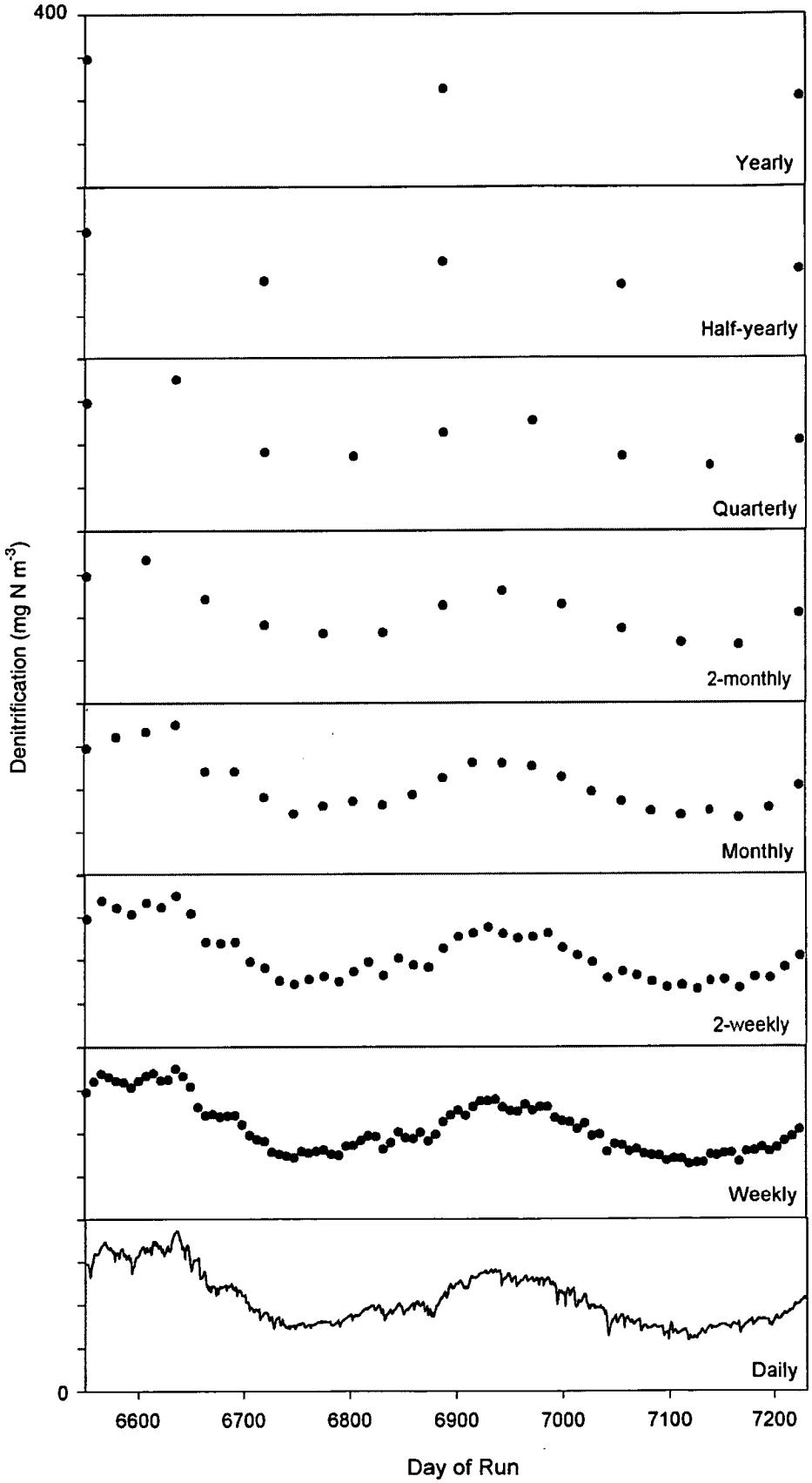
As would be expected, reducing the frequency of sampling reduces the amount of variation observed in the system (e.g. consider the time-series for bay-wide denitrification in BM2 and IGBEM in Figure 4.7). Two-weekly or even monthly sampling removes much of the noise present in the daily samples, but still reveals the underlying trend. Decreasing the frequency further to half-yearly or annual sampling leads to a substantial loss of useful information.

Figure 4.7: Time-series of denitrification as defined by each of the sampling frequencies for

(a) Bay Model 2



(b) the Integrated Generic Bay Ecosystem Model



The effect of apparently reducing variance can have a marked effect on estimates of system-level measures. For example, using sampling frequencies of one or two months cause time-averaged primary production to be overestimated, while longer sampling frequencies often yield substantial underestimates (Figure 4.8). The problem is exacerbated if the sub-samples coincide with extreme peaks or troughs in the series.

The issue of the effects of sub-sampling is much stronger for groups or processes with fast dynamics (many events or generations per year) while estimates involving slower growing groups are not as heavily affected. For example, the estimate for mean production of benthic filter feeders is only marginally affected by sampling frequency (Figure 4.9).

Changing the external forcing of the system (i.e. nutrient loads and fishing rates) does not have a consistent effect across all groups, and different changes to forcings yielded dissimilar results (Table 4.7). Reducing the nutrient load weakens the effects of sampling frequency as much of the variation in the system is removed; i.e. there are fewer, short-term, high-magnitude fluctuations in denitrification, biomass and productivity. When the nutrient load is increased the inaccuracy introduced by using longer sampling frequencies is substantially increased for measures associated with the primary producer and planktonic groups, particularly in IGBEM (e.g. water column primary productivity (Figure 4.10)). The inaccuracy of measures (e.g. productivity) for the other groups, such as the fish and sediment fauna, shows no real change with increasing nutrient load. The ratio of the true value to estimates based on longer sampling frequencies changes by less than 1% for these measures. In contrast, a reduction in fishing pressure and the resulting shifts to higher biomasses and stronger interactions between groups causes an amplification of the effects of using longer sampling frequencies, particularly for the fast-lived groups and associated processes (e.g. water column secondary productivity (Figure 4.11)), but it has little effect on

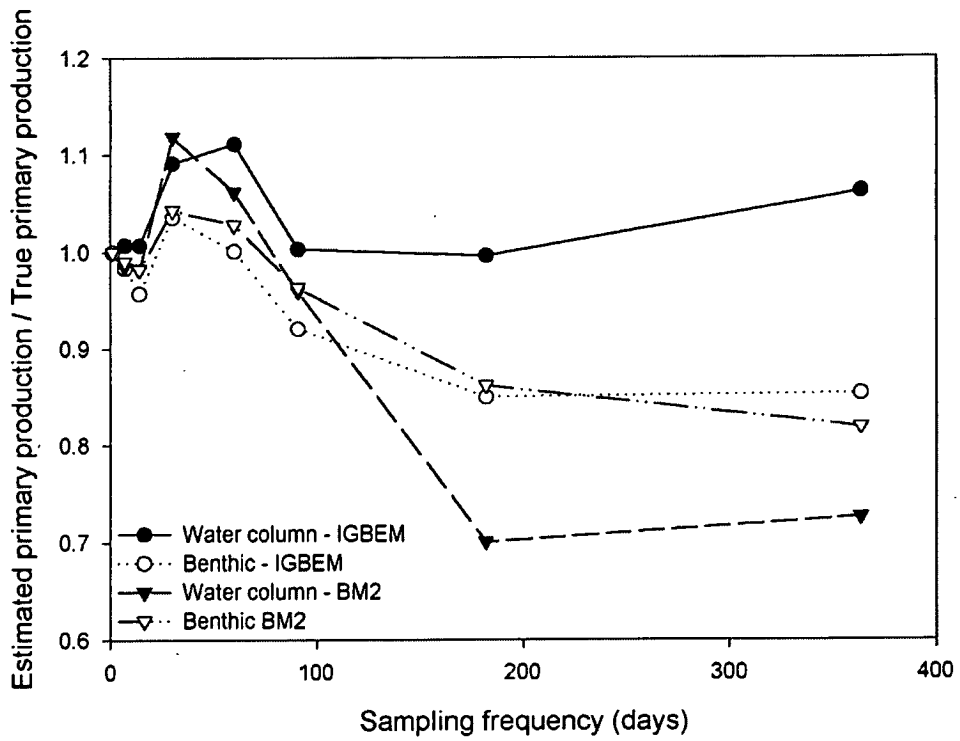


Figure 4.8: Ratio of the estimated and true values of pelagic (water column) and benthic primary production for Bay Model 2 (BM2) and Integrated Generic Bay Ecosystem Model (IGBEM) under various sampling frequencies.

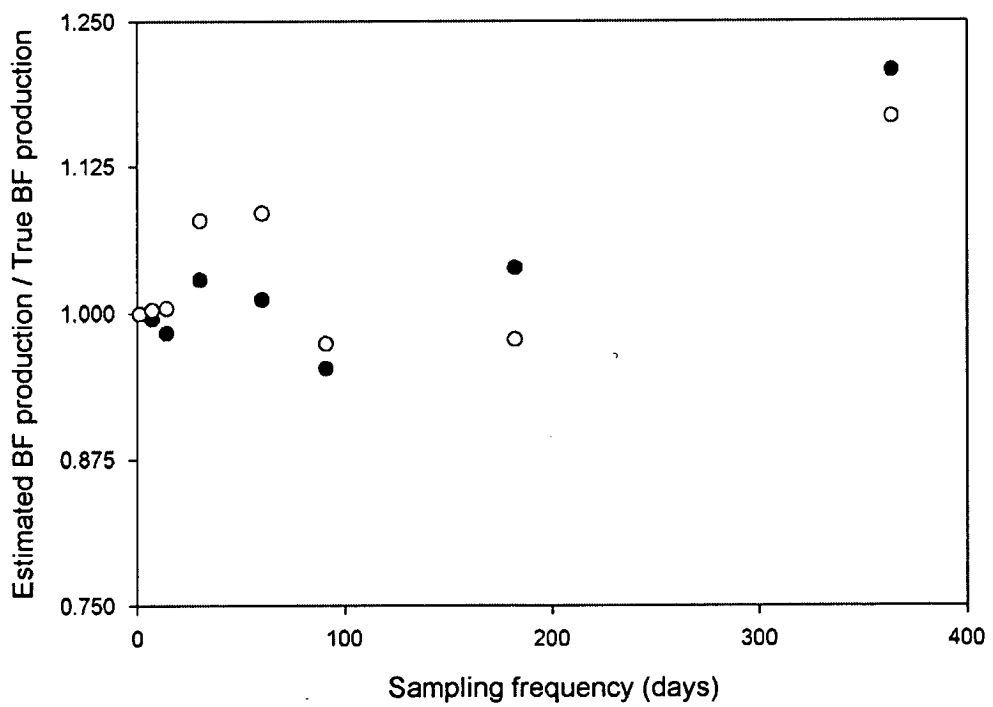


Figure 4.9: Ratio of the estimated and true values of production by benthic filter feeders (BF) for Bay Model 2 (open circles) and Integrated Generic Bay Ecosystem Model (solid black circles) under various sampling frequencies.

Table 4.7: Summary of the impact of changes in nutrient loading or fishing pressure on the effects of sampling frequency.

Change in Conditions	Impact
Decreased nutrient loading	Reduced effect of sampling frequency as less variation translates to less inaccuracy when using longer sampling frequencies
Increased nutrient loading	Increase in the effects of sampling frequency, but only for the groups with fast-dynamics
Decreased fishing pressure	Increase in the effects of sampling frequency for the harvested groups and prey groups with fast-dynamics
Increased fishing pressure	Reduced effect of sampling frequency for the harvested groups. No change in the effects on other groups, unless the sampling frequency aligns (aliases) with fluctuations in prey biomass caused by the establishment, prior to fish-down, of new recruits to the fished stocks – this is particularly a problem with annual sampling.

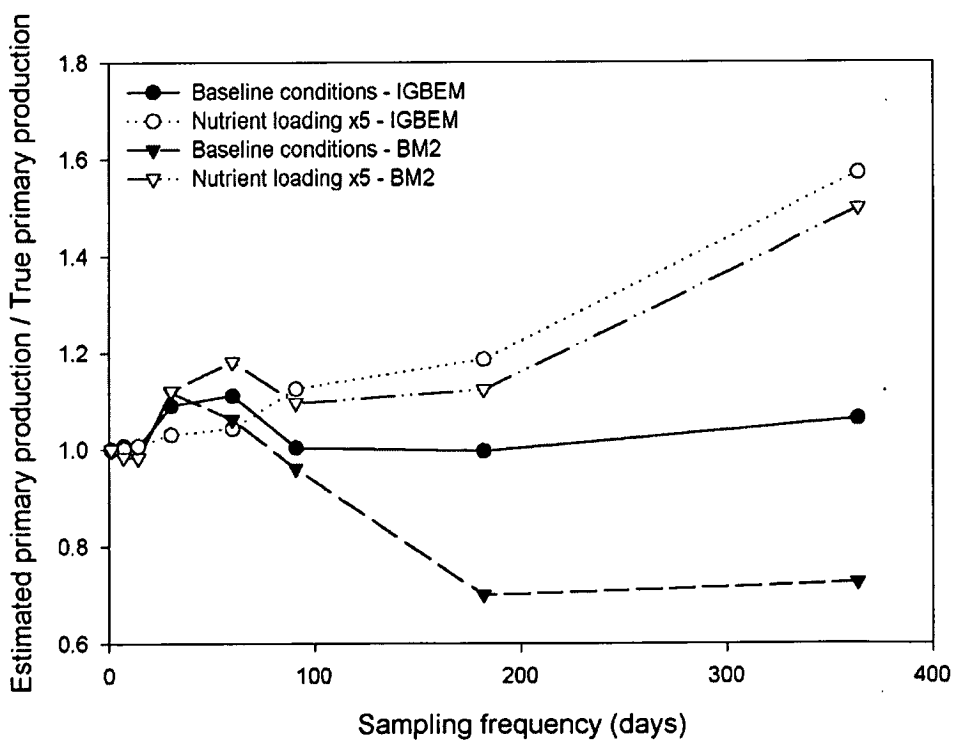


Figure 4.10: Ratio of the estimated and true values of pelagic primary production for the Integrated Generic Bay Ecosystem Model under various sampling frequencies with baseline nutrient conditions and a fivefold increase in nutrient load.

denitrification estimates. Again, this effect is stronger in IGBEM. Lastly, an increase in fishing pressure reduces the effects of using longer sampling frequencies, especially for the harvested groups, as their depleted biomasses show less variation through the year. Measures associated with prey groups, which may be released from predator control with an increase in fishing, do not show any increased effects of using longer sampling frequencies under higher fishing loads, except when annual sampling regimes are employed. At this point, aligning (aliasing) sampling times with peaks or troughs in the fish stocks can cause distortion of estimates, particularly for groups with fast dynamics. Under heavy fishing, if sampling coincides with a point just prior to recruitment, when stocks of fish are low, then estimates of the biomass or production of prey groups may be substantially overestimated (by as much as 50%). The converse holds if annual sampling coincides with the short period when recruits are of sufficient size to depress prey populations, but before fishing depletes their numbers to the point that their main prey groups recover.

4.4 Discussion

4.4.A Spatial structure

Harris et al. (1996) found that there is a decrease in local variation on less spatially resolved geometries for the original Port Phillip Bay Integrated Model (PPBIM). This matches the observation that BM2 and IGBEM display more short-term fluctuation when applied on more spatially resolved geometries. The mechanisms identified by Harris et al. (1996) for the behaviour of PPBIM also explains the corresponding behaviour of BM2 and IGBEM. The first of these is that more finely resolved spatial resolution results in a higher degree of local variation in environmental conditions due to changes in advection and mixing along broad-scale gradients produced by the location of the point source inputs. Secondly, point source inputs will

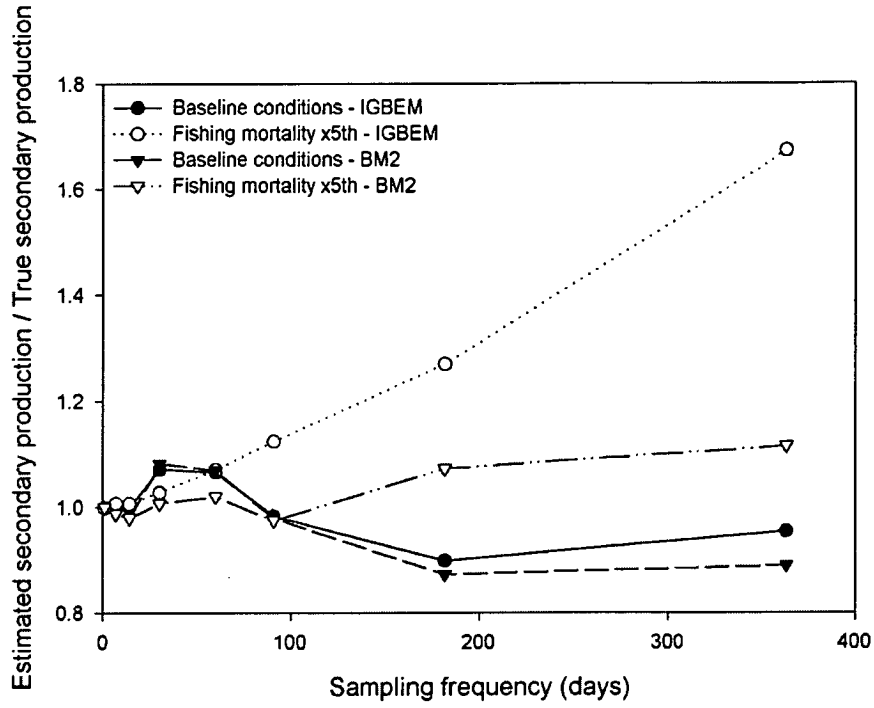


Figure 4.11: Ratio of the estimated and true values of pelagic secondary production for the Integrated Generic Bay Ecosystem Model under various sampling frequencies with baseline fishing conditions and a fivefold decrease in fishing pressure.

have a larger local, short-term influence when spatial resolution is finer as the inputs are not immediately diluted by mixing with sizeable proportions of the total capacity of the bay, as is the case on the coarser resolutions. Lastly, advection on the more detailed geometries continually brings local communities into contact with new levels of nutrients. Thus, these groups can never reach steady state as they are in a perpetual state of flux. As a result of these mechanisms, the less spatially resolved geometries underestimate local variation as they damp the many influences of environmental heterogeneity and allow the planktonic groups to inappropriately attain steady state.

The decrease in variation with coarser spatial resolution is reminiscent of the drop in the variation in the observed output of cellular-automata predator-prey models when increasingly large observation windows are used (e.g. Pascual and Levin 1999). However, Pascual and Levin's work differed from ours in that they considered the same

total number of cells and only changed the size of their observational windows, while this study considered different numbers of cells describing the same total area. Both methods remove heterogeneity. By averaging, Pascual and Levin (1999) smooth out local heterogeneity in population sizes at the time of "sampling", while the models in this study remove heterogeneity in population sizes and local environmental conditions by using fewer larger cells in the less spatially resolved geometries.

The most pronounced impact of removing heterogeneity when applying models on the coarser geometries is the tendency for self-simplification of the food webs. Collapse of the web in this way is produced by two interacting consequences of the smearing of environmental conditions with coarser spatial resolution. The first is that changing spatial resolution produces systems with differing depth profiles and nutrient, chemical and hydrodynamic properties. Coarser geometries do not have the steep depth gradients seen in the 59-box model and so, for example, sediment light levels are more conducive to widespread seagrass populations rather than the restricted populations seen in the 59-box model. More importantly, the flushing time of the bay for coarser geometries is much shorter than in the 59-box model. With a drop in resolution over the southern boxes around the bay mouth, flushing time drops from more than 270 days for the 59-box geometry to less than 93 days for the 3-box model (Walker and Sherwood 1997). It was not possible to calculate flushing time for the 1-box model. However, it must be noted that, like the boxes at the mouth of the bay in more complex geometries, the 1-box model shows tidal aliasing and so the exchange between the boundary conditions of Bass Strait and the bay as a whole are over-stated. Flushing time and other environmental conditions have direct habitability effects on at least some of the biological components of the system and this alone could produce differing dynamics (including extinction) depending on the geometry used. That the differing geometries capture different physical environments is highlighted by the relative responsiveness of

the two models. BM2 requires retuning for numerical stability when the spatial resolution is changed, while IGBEM does not. This is in keeping with previous work that has found that BM2 needs more tuning as the underlying physical conditions change (chapters 2 and 3).

The "smearing" of the physical conditions with reduced spatial resolution has an additional biological effect. The removal of boxes and the general homogenisation of conditions removes refugia that allowed the persistence of some groups. For instance deposit feeders and meiobenthos, which are competitors but also predator and prey, are spatially disjunct in the 59-box case. The deposit feeders line the edge of the bay while the meiobenthos inhabit the deeper areas of the bay. With coarser geometries this spatial partitioning is not possible and the meiobenthos is completely excluded. This is a direct result of the use of differential equations in the model. Within each box competitors and predators are effectively "everywhere" and encounter rates are not related to abundance as they are in nature. The functional response used for grazing does include an "availability" parameter, but as this is a fixed proportion of the prey biomass the equations do not inherently include many refuges or lags. However, these refuges may be added by using a spatially resolved system, as differential abundance across the boxes creates lags and refugia. As a result the full trophic web is supported when the models are run on spatially resolved geometries, but the web collapses when coarser geometries are used. This effect of spatial resolution on trophic stability is particularly important given that many of the traditional models considering the effects of system complexity have omitted it (May 1974, Pimm 1982, Cohen and Newman 1988).

More recent work with spatial models shows different and multifaceted relationships between complexity, stability and invasiveness. As observed in nature, the relationships depend on network topology (the magnitude and direction of biological interactions between network members) (Dunstan and Johnson submitted). These recent

models still use assumptions that are unrealistic and there has been speculation over whether the findings from conventional consideration of the effects of trophic complexity would hold if more realistic conditions (including nutrient conservation, spatial structure and coupling, temporal forcing, omnivory, detrital infusion, ontogenetic diet shifts and mixotrophy) are included in the models (May 1974, Leibold 1996, Polis and Strong 1996, Keitt 1997). The models considered here include these processes.

Self-simplification of the food webs with a reduction in spatial resolution seen in this study suggests that a large number of trophic groups does not destabilise the system when environmental heterogeneity is present, but when the heterogeneity is removed the additional reticulation and detail in the food web cannot preserve the system and the web collapses. This implies that spatial heterogeneity is one form of complexity that is a required part of the theoretical consideration of realistic food web dynamics and community structure. Dunstan and Johnson (submitted) reach similar conclusions for competition systems, and modelling work by Keitt (1997) and Donalson and Nisbet (1999) also indicate that species persistence increases with system size and heterogeneity. They posit that larger systems have a greater capacity for ephemeral refugia, as physical and biological fluctuations in different regions can be out of phase. This is not possible in smaller systems so these systems go extinct. This is one of the mechanisms underlying the responses observed here.

The biological components included in the biogeochemical model of PPB (PPBIM) constructed as part of the Port Phillip Bay Environmental Study are largely from those groups that show the least impact of spatial structure, with macroalgae notable as the single exception. This is not surprising given that Murray and Parslow (1997) carefully selected the web structure in PPBIM to allow for maximum stability. It may also explain why Murray (2001) found a 1-box version of PPBIM very helpful during the development of the full model, whereas a similar approach would not be as

useful when trying to consider the full web that underlies IGBEM and BM2.

One area in which Murray (2001) and the findings here agree is in model divergence with changing conditions. Murray (2001) illustrated the limitations of the "simple modelling approach" by comparing the 1-box and 59-box versions of PPBIM under increasing nutrient loads. It was found that as conditions changed the 1-box model no longer reflects the dynamics of the 59-box model, as different processes emerge as important in the two cases. Spatial variation proves to be a crucial determinant of bay dynamics as the PPBIM model system moves from a mesotrophic to a eutrophic state (Murray 2001). Similarly, trends in the effect of spatial structure noted under baseline conditions of BM2 and IGBEM do not hold as nutrient loads and fishing pressure changes. For example, under an increase in nutrients, the standard 59-box run of BM2 predicts that seagrass will effectively become extinct throughout the bay. This is not the case when using simpler geometries, where it persists despite the change in nutrient levels. In the less spatially resolved cases seagrass biomass is reduced and the magnitude of interannual cycles is increased with increased nutrient loading, but only the 8-box model gives any indication that the distribution would contract and that the population would be in danger of disappearing from the bay. Thus, as is the case with PPBIM, complex system behaviour introduced by spatial heterogeneity cannot be ignored if the models are to be used to evaluate the impact of changing conditions.

4.4.B Sampling frequency

Despite differences in the models, and either damping or enhancing of variation by different sampling scenarios, there is a consistent pattern as to the usefulness of the various sampling frequencies (Table 4.8). At one extreme there are potentially large inaccuracies introduced by half-yearly or annual sampling, while at the other the noise inherent in daily sampling does not justify the immense storage requirements (or

expense) associated with computer generated or empirical observations of this detail. Under the circumstances considered here, of no observational error and complete knowledge, sampling frequencies of a week to a month are optimal. The lower end of this range agrees with field studies that have indicated that weekly sampling is best for measures such as primary productivity and sediment oxygen (Taylor and Howes 1994, Rantajärvi et al. 1998). These field studies do not find the monthly sampling as reliable as does the model study. The forcing files used in BM2 and IGBEM do not capture all of the temporal variability seen in real systems. The extra variation in natural systems may overwhelm the usefulness of monthly sampling suggested by the models.

The model and field studies point to similar conclusions regarding the effects of a poorly chosen sampling frequency. If longer sampling frequencies are implemented then estimates can be inaccurate and misleading with regard to understanding system dynamics. These concerns are particularly important when deciding on monitoring schemes as part of a system wide management strategy. Logistics may mean that sampling on the order of 7 to 14 days is impractical and prohibitively expensive. Unfortunately, evidence from field studies (Taylor and Howes 1994, Rantajärvi et al. 1998, Bennion and Smith 2000) and the work presented here indicates that opting for longer sampling frequencies is inadequate for informed management. This is particularly true for events that can happen very quickly, but have long lasting effects, such as oxygen-crises in the sediment. If longer sampling frequencies are to be successful in the future an index of overall system state which is robust to sampling frequency needs to be found. No such index was identified in this study, but it is likely that if one exists it will be a variable with slower dynamics.

Table 4.8: Summary of the utility of a range of sampling frequencies.

Daily	Weekly	2-weekly	Monthly	2-monthly	Quarterly	Half-yearly	Annually
Dominated by noise, which can mask underlying trends. This frequency does not add much to what can be captured by weekly sampling, except when trying to track oxygen stress events, which can occur for less than a week, but have long lasting impacts.	These frequencies are very similar with regard to the amount of information captured (and consequently any conclusions drawn).		Similar to weekly and fortnightly, but monthly sampling does lose some of the short-term variation. It is also important to be aware of potential aliasing problems. Overall, it still captures the seasonal trends well.	The loss of information is becoming evident for the groups with fast dynamics (seasonal trends are becoming "saw-toothed"). Satisfactory for groups with slow dynamics (much of the larger benthos)	Loss of information is evident for all groups, though those with fast dynamics are impacted the most.	These frequencies miss important events and much of the seasonal information. Aliasing is a critical problem. Sampling at these frequencies can lead to inaccuracies in estimates of annual denitrification, production and consumption of more than 25 – 50% depending on the ambient conditions. This is particularly true for measures associated with groups with fast dynamics (such as the plankton).	

4.5 Conclusions

Spatial and temporal resolution is a critical issue when considering the dynamics of ecosystems. The complex and emergent features of ecosystem behaviour mean that there are strong limitations on minimum sampling effort in time and space. Removing complexity, by sampling on long time scales or using coarse spatial dimensions relative to the dynamics of the system, is a two edged sword. The scale at which sampling is undertaken not only impacts upon the costs of a field sampling program, it can also influence the processes detected and how they are interpreted. An observation scheme that reduces costs by concentrating on large spatial and temporal scales may miss crucial mechanisms that occur on a fine scale, but have far reaching impacts (e.g. oxygen crises). Moreover, modelling and field studies indicate that space itself is an important resource in an ecosystem and ignoring it can have a substantial impact on conclusions drawn.

The impacts of scale are not only an important concern in the field, but they can have substantial influences on modelling too. By simplifying model systems and increasing the scale at which variation is considered, storage requirements are reduced drastically, calibration time falls sharply and some trends are easier to discern. However, this comes at the cost of losing crucial emergent properties, the ability to capture the full web structure and changing importance of mechanisms that appear to characterize natural systems. Models need not be highly resolved, but to be informative the spatial and temporal resolution employed must allow for expression of the dominant gradients and dynamics in the system. As pointed out by Polis and Strong (1996), complexity and variation may be inconvenient to a theoretical understanding of ecosystems, but they may also be two of the most important driving forces of those systems. Without their inclusion it may be impossible to use models to understand systems and how they respond to change.

Chapter 5 Lump or chop: The effect of aggregating or omitting trophic groups on the performance of ecosystem models

Abstract

As ecosystem models become more commonly applied, questions regarding optimal complexity and parsimonious methods of simplification arise. Simplification of the underlying trophic complexity is one viable approach. Two potential methods of achieving this are to omit or aggregate components in the simulated food web. When applied to two biogeochemical ecosystem models, it was found that if the system is already aggregated to the level of functional groups then further aggregation will not work as well as the strategic omission of less important groups. The relationship between simplification and performance is nonlinear, but it is possible to identify two general principles. First, over-simplification of the web leads to poor model performance. Second, if important processes or couplings (such as between the pelagos and benthos in shallow coastal systems) cannot be included explicitly, simple forcing is unlikely to be a reliable alternative. Some form of robust empirical representation will be necessary.

The results of model simplification also have implications for the ecological stability-diversity debate. Shifts in the relative importance of different groups with changing ecosystem conditions, and dependence of the effect of simplification on ecosystem state, support the concept of the ecological "insurance hypothesis". The models used here do not support the idea of a simple relationship between connectance or interaction strength and the stability of system behaviour. The biological details of the web, the trophic and non-trophic, direct and indirect interactions included are a crucial determinant of ecosystem and model behaviour that cannot be ignored.

Keywords: trophic complexity, trophic structure, aggregation, omission, stability, diversity, biogeochemical, ecosystem, model, IGBEM, BM2

5.1 Introduction

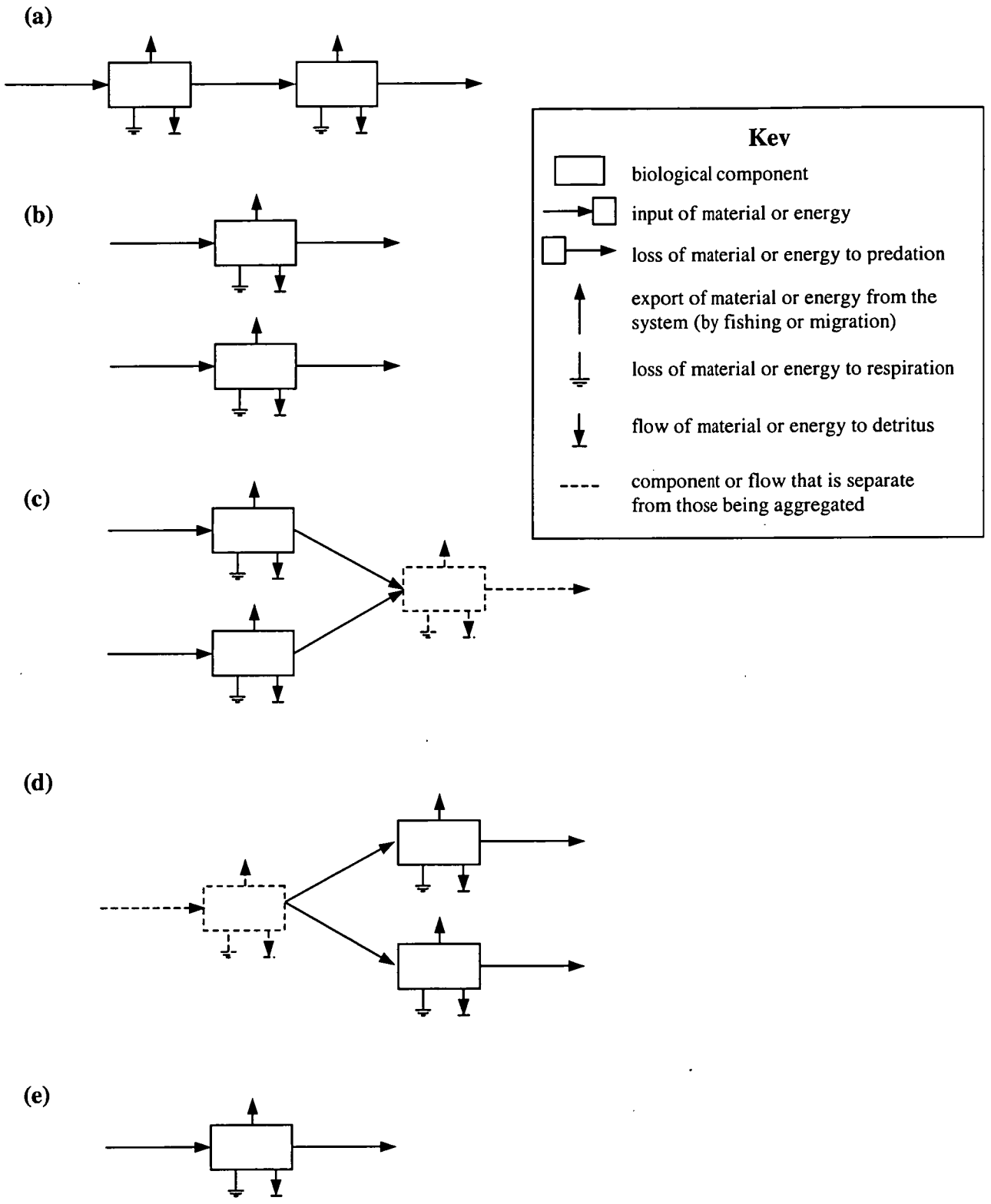
Natural ecological systems are inherently complex and it is neither possible nor desirable to model them exactly. Increasing focus on using ecosystem models as an integrated part of fisheries, water quality and general system level management has highlighted the importance of the issue of simplification. Simplified models have a number of desirable characteristics. They are often easier to comprehend (Iwasa et al. 1987), they can be economically or logistically attractive as they require less input information (Sugihara et al. 1984), and they are less computationally intensive (Lee and Fishwick 1998). Ludwig and Walters (1985) have also shown that simplified models can be more effective than more complex versions, as the simpler models do not suffer as much error propagation or sensitivity to parameterisation. Another potential advantage of simplified models, particularly aggregated ones, is that they are not tied to individual species and so, by definition, are more generic. Consequently, they may be more robust to change and amenable to application. Simplifications must be made and one way in which this can be done is by simplifying the underlying food web.

Model simplification by aggregation involves simplifying the model (and associated food web) by combining components that share common predators, prey or other characteristics. Given the universal use of aggregation in ecology it is not surprising that it has received some attention within the areas of theoretical systems ecology (O'Neill and Rust 1979, Iwasa et al. 1987) and biogeochemical modelling (Zeigler 1976, Cale and Odell 1980, Gardner et al. 1982, Cale et al. 1983). A common finding across many studies is that components of a system may be aggregated with little error if the property being scaled is highly correlated among the components

(Bartell et al. 1988), or if their rate constants are similar (Wiegert 1977, O'Neill and Rust 1979, Cale and Odell 1980, Gardner et al. 1982, Cale et al. 1983, Iwasa et al. 1987), or if one of the components is consistently comparatively rare (O'Neill and Rust 1979, Cale et al. 1983). However, it is also recognised widely that because an aggregate is not capable of producing exactly the same behaviour as the constituent components, errors due to inappropriate aggregation can be excessive (O'Neill 1979, Cale and Odell 1980, Gardner et al. 1982, Cale and O'Neill 1988, Iwasa et al. 1987, Rastetter et al. 1992). For example, aggregating components that are serially linked (Figure 5.1a) is ill advised in most cases, while aggregating components that are in parallel (Figure 5.1b), or share a common predator or prey (Figures 5.1c and 5.1d), is usually acceptable if their rate constants are within two- or threefold of each other (Gardner et al. 1982). It has also been found that if aggregated parameters cannot be measured accurately then the compounding effects of aggregation and measurement error result in significant output error and poor model performance (Gardner et al. 1982, Rastetter et al. 1992).

An alternative method of model simplification is reduction in model complexity by omitting, rather than aggregating, components. This method follows from the suggestion that system behaviour may be characterised by the dynamics of dominant, or representative, species. Despite being central to the concept and use of indicator species, this approach has not received the same level of theoretical and modelling attention as simplification by aggregation. There is little work that directly considers the effects of omitting groups on model performance, and the implication for the use of models simplified in this way. The work that has been done has largely concentrated on models using randomly constructed food webs to investigate the effects of diversity on system stability (May 1973), or food chain models where entire trophic levels are considered rather than individual species or guilds (Carpenter and Kitchell 1993), or models of plankton ecology (Yool 1998, Edwards 2001). Conclusions pertaining to more complete

Figure 5.1: Diagrams of the most common system configurations that are simplified by aggregating groups: (a) in series, (b) in parallel, (c) triangular with a shared predator, (d) triangular with a shared prey and (e) the aggregated form (identical for all).



or realistic ecosystem models may be drawn by considering changes in model performance as models are constructed incrementally (e.g. ERSEM I vs ERSEM II (Baretta et al. 1995, Baretta-Bekker and Baretta 1997)). The "insurance" or "redundancy" hypothesis (Yachi and Loreau, 1999) suggests that without any change in ecosystem conditions at least some of the redundant species or groups could be removed without the system changing substantially. However, the idea that overall mean interaction strength is closely linked to system behaviour implies that removing a single species could cause a significant shift in system dynamics (McCann 2000). Work by Yodzis (2000) on the diffusion of the effects of interactions through food webs supports the idea that, at least in some ecosystems, considering only a small subset of the food web is inappropriate as even the influences of small perturbations will not be represented accurately. However, the issue is far from resolved. Those studies considering the effect of trophic complexity on models of plankton ecology indicate that some simplification is possible, e.g. models that omit bacteria and certain nutrient groups still perform well (Yool 1998), but the effects of simplification can be dependent on the linkages captured in the modelled web (Edwards 2001). However, because the food webs included in the full versions of these plankton models are very simple, more work considering larger and more realistic food webs is necessary.

The greatest interest in the effects of trophic complexity on ecosystem models was born of the modelling efforts associated with the International Biological Program (e.g. O'Neill 1975, Watt 1975 and Wiegert 1975). However, it has a wider place within theoretical ecology in the long running debate over the relationship between stability and diversity in food webs. Historically, field studies suggested that an increased number of biological components would confer greater stability on a community (Odum 1953, MacArthur 1955, Elton 1958). In contrast, some mathematical studies suggested the opposite and indicated that randomly constructed model communities tended to

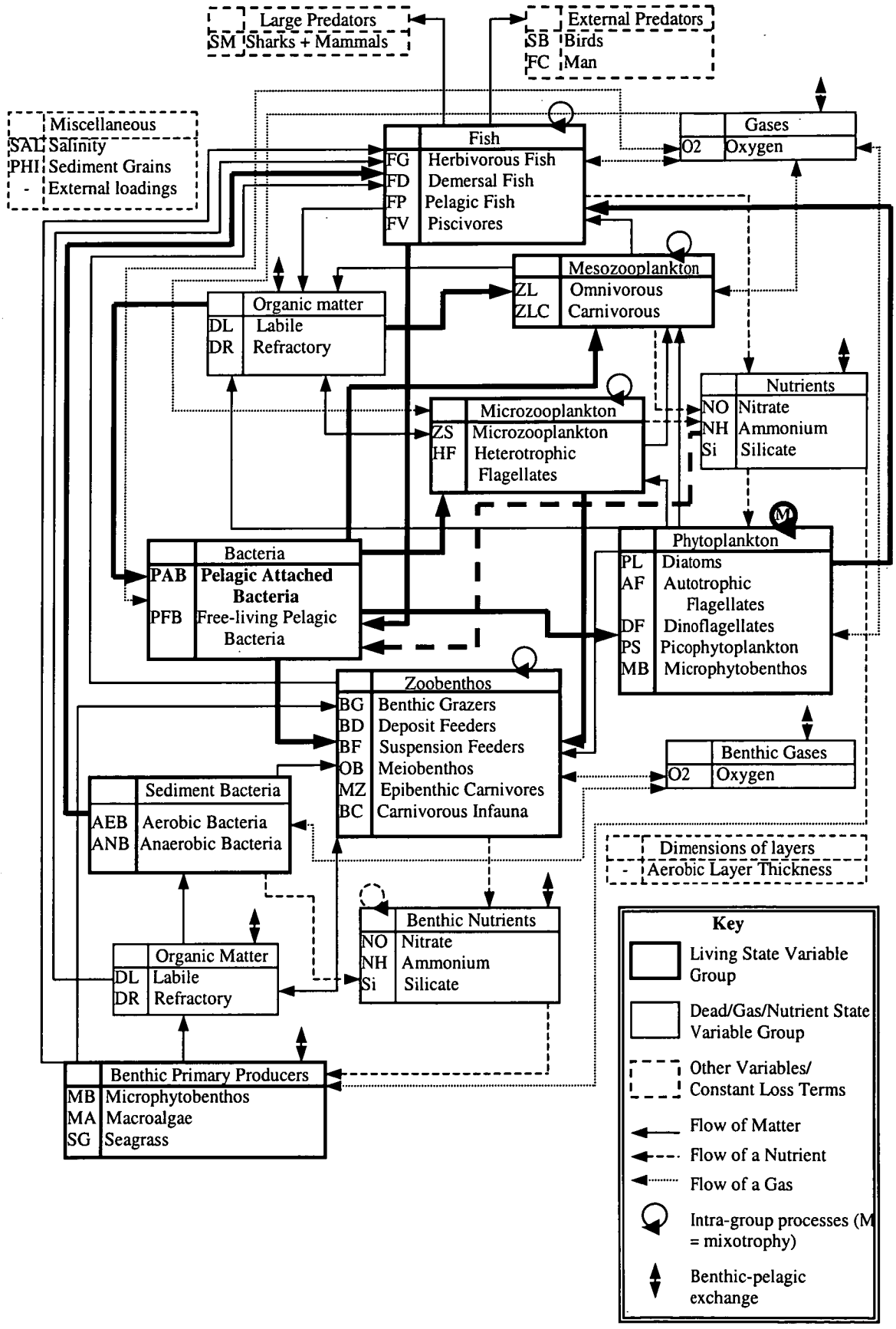
destabilise as they became more complex (Gardner and Ashby 1970, May 1973, Pimm and Lawton 1978). Later studies have shown that these two sides of the problem are not inconsistent as natural systems are not constructed randomly and are characterised by a large number of buffering mechanisms, as well as material conservation and external dependencies or linkages (De Angelis 1975, Yodzis 1981, Tilman and Downing 1994, Sterner et al. 1996, McCann et al. 1998, Harding 1999). However, the debate is not yet resolved and the consideration of models using more realistic food webs, constraints (e.g. material conservation) and physical forcing still has much to offer, given that it is doubtful that there is a simple relationship between diversity and stability when more realistic systems are considered. If theories such as the "weak interaction effect" (McCann 2000) are correct, it is likely that simplification of a system will take the system through alternating periods of increased and decreased stability as the ratio of strong:weak interactions is modified in one direction or another. Monitoring the behaviour of models under a series of simplifications may help to give some insight on this topic.

Here we report the effects of model simplification by aggregating or omitting groups in two biogeochemical ecosystem models. The work and ecosystem models used are part of a larger study on the effects of model structure and complexity on the performance and behaviour of ecosystem models.

5.2 Methods

To investigate the effects of trophic complexity on model performance the food web (Figure 5.2) implemented in two biogeochemical ecosystem models is modified in a number of ways, while other features of the models (e.g. spatial resolution, stoichiometry, processes included) are left unchanged. The two models are Bay Model 2 (BM2) (chapter 2) and the Integrated Generic Bay Ecosystem Model (IGBEM) (chapter

Figure 5.2: Food web diagram for the ecosystem models Bay Model 2 (BM2) and the Integrated Generic Bay Ecosystem Model (IGBEM). The Pelagic Attached Bacteria and any flows marked in bold are present in BM2, but not in IGBEM.



1). The two models share a similar list of biological components (Table 5.1), which represent the typical list of functional guilds found in a temperate bay system. Both models include the same biological, physical and chemical processes, but in differing degrees of detail (Table 5.2).

Table 5.1: List of the biological components in the full versions of Bay Model (BM2) and the Integrated Generic Bay Ecosystem Model (IGBEM).

Component	Codename
Diatoms	PL
Autotrophic flagellates	AF
Picophytoplankton	PS
Dinoflagellates	DF
Free-living pelagic bacteria	PFB
Pelagic attached bacteria (BM2 only)	PAB
Heterotrophic flagellates	HF
Microzooplankton	ZS
Large omnivorous zooplankton	ZL
Large carnivorous zooplankton	ZLC
Planktivorous fish	FP
Piscivorous fish	FV
Demersal fish	FD
Demersal herbivorous fish	FG
Macroalgae	MA
Seagrass	SG
Microphytobenthos	MB
Macrozoobenthos (epifaunal carnivores)	MZ
Benthic (epifaunal) grazers	BG
Benthic filter feeders	BF
Infaunal carnivores	BC
Benthic deposit feeders	BD
Meiobenthos	OB
Aerobic bacteria	AEB
Anaerobic bacteria	ANB

Table 5.2: Processes and structure of Bay Model 2 (BM2) and the Integrated Generic Bay Ecosystem Model (IGBEM).

Feature	BM2	IGBEM
General features		
Biomass units	mg N/m^3	mg/m^3 of C, N, P, Si
Input forcing	nutrients and physics on interannual, seasonal, tidal frequencies	nutrients and physics on interannual, seasonal, tidal frequencies
Level of group detail	functional group	functional group
Process related		
Bioturbation and bioirrigation	yes	yes
Consumption formulation	type II	mixed (type II, type III)
Formulation detail	general: only growth, mortality and excretion explicit	physiological: the processes of assimilation, basal/ activity/stress respiration, defecation, excretion, ingestion, mortality are all explicit
Light limitation	optimal irradiance fixed	phytoplankton can acclimate to ambient light levels
Mixotrophy	dinoflagellates	none
Nutrient limitation	external nutrients determine uptake	internal nutrient ratio determines nutrient uptake and disposal
Nutrient ratio	Redfield	internal specific nutrient ratio
Oxygen limitation	yes	yes
Sediment burial	no	yes
Sediment chemistry	dynamic, with sediment bacteria	empirical, sediment bacteria are a tracer only
Shading of primary producers	yes	yes
Spatial structure	flexible with the potential for multiple vertical and horizontal cells	flexible with the potential for multiple vertical and horizontal cells
Temperature dependency	yes	yes
Transport model used for hydrodynamics flows	yes	yes
Model closure		
Top predators represented by static loss terms	yes	yes
Linear mortality terms	yes	yes
Quadratic mortality terms	yes	no
Fish and fisheries related		
Age structured fish	9 age classes	9 age classes
Fishery Discards	target species only	target species only
Invertebrate fisheries	yes	no
Stock-recruit relationship	constant recruitment	constant recruitment
Stock structure	external: the reproductive stock outside the bay produces the recruits and the oldest age classes migrate out of the bay to join this stock	external: reproductive stock outside the bay produces the recruits and the oldest age classes migrate out of the bay to join this stock

Briefly, IGBEM is a physiologically explicit biogeochemical process model, which follows the carbon, nitrogen, phosphorus and silicon pools of its biological components (chapter 1). It was constructed using the physical and biogeochemical submodels of the Port Phillip Bay Integrated Model (PPBIM) (Murray and Parslow

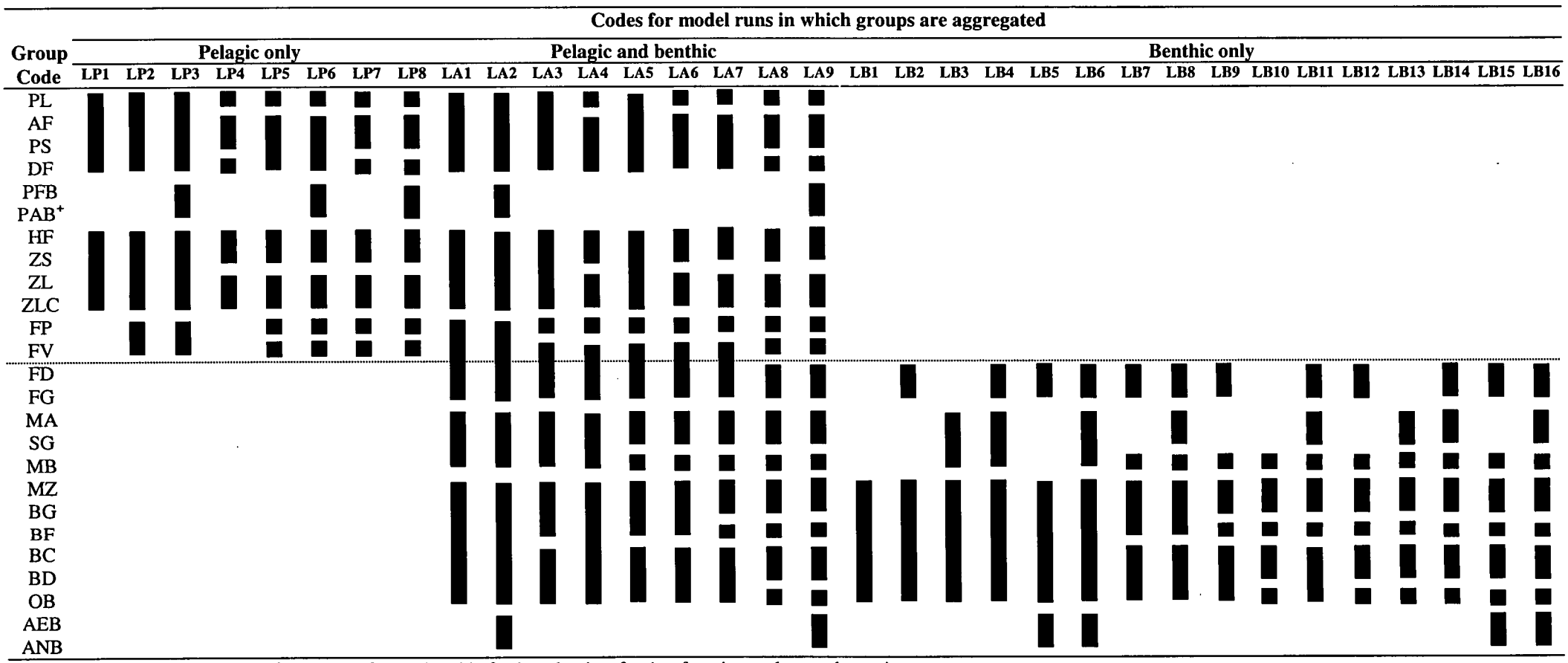
1997, 1999a) and the biological groups of the European Regional Seas Ecosystem Model II (ERSEM II) (Baretta et al. 1995, Baretta-Bekker and Baretta 1997). The benthic primary producers included in PPBIM were retained in IGBEM, as there was no analog present in ERSEM II. In addition, herbivorous benthic invertebrates and fish were added, using the same general formulation structure as ERSEM, to exploit the benthic primary production and complete the food web.

In comparison with IGBEM, BM2 has much less process detail, using relatively simple general equations of assimilation and waste handling, and only representing the nitrogen and silicon pools of the biological components. This formulation was the one used in PPBIM, and BM2 was developed by extending that formulation to cover all of the groups in IGBEM (chapter 2).

5.2.A Aggregating functional groups

When components and their associated links are aggregated all the original linkages to the separate components are kept but directed to the aggregated group. The parameter values used for the aggregated group represent the weighted average of the parameters for the constituent components. Thirty-three simplifications of the web structure are made by aggregating components (Table 5.3). These simplifications reflect aggregations made in other field and model studies (for example "other benthos" is a common feature of the ECOPATH models primarily concerned with finfish, but which attempt to include a broad picture of the entire web (Christensen 1992)). We consider a range of intensity of amalgamation, from slightly aggregated cases to a massively reduced web with only phytoplankton, zooplankton, fish, benthos and macrophyte aggregated groups. The aggregated webs also span cases where only the pelagos or benthos is considered. Thus, some runs include only pelagic components, while others have only benthic components (apart from a pelagic food group, which is a forcing

Table 5.3: List of the trophic simplifications of the food web made by aggregating groups. Bars indicate groups lumped together in constructing aggregated groups. Codes for the base groups are given in Table 5.1. "Pelagic only" runs only include the pelagic fraction of the food web, "Pelagic and benthic" runs include pelagic and benthic groups, and "Benthic only" runs only include the benthic fraction of the food web. Note that all the groups above the dotted line are considered to be pelagic components and all the groups below the dotted line are considered to be benthic components.



* A generic water column food group for the benthic feeders that is a forcing function and not a dynamic group.

+ Bay Model 2 only. In the Integrated Bay Model the Pelagic Free Bacteria alone were present in the "pelagic bacteria metagroup".

function). For ease of reference, each of the runs using aggregated webs has a code (listed in Table 5.3). These codes begin with L, the second letter indicates the fraction of the ecosystem considered (P for pelagic only, B for benthic only, and A for benthic and pelagic), and the number represents the degree of aggregation (the lower the number the more highly aggregated the model web).

5.2.B Omitting functional groups

When a group is omitted from the web there are no re-parameterisations of the remaining components or changes in model formulations, with two exceptions. When a predatory group is removed from the web, the mortality parameters of its prey groups are adjusted to implicitly include the predation pressure that was explicit when the predator was still active in the web. Second, when bacteria are omitted from BM2 runs, the empirical model of denitrification proposed by Murray and Parslow (1999a) for PPBIM is used in place of the sediment chemistry module that was dependent on bacteria. This empirical sediment chemistry model is standard for all runs of IGBEM. Overall, twenty-one simplified forms of the original web are made by omitting groups (Table 5.4). These range from the complete omission of all but two of the components to the omission of only a few components, primarily those that are not as commonly included in system models. One special class of omission is truncation. The most common form of truncation is when either the lower or top ends of the trophic web are removed (e.g. consider the pelagic groups of OP1, where every group above zooplankton is omitted). The list of simplified forms includes examples of truncation. Another form of truncation is when an entire subweb is dropped, restricting the coverage of the web to certain habitat types. For example, some runs include only pelagic biological components (though the sediment chemistry and detritus pools remain), while others have only the benthos as dynamic components (a pelagic food

Table 5.4: List of the trophic simplifications of the food web made by omitting groups. "Y" indicates inclusion of the group in that version of the modified food web. The codes for the groups are given in Table 5.1. "Pelagic only" runs only include the pelagic fraction of the food web, "Pelagic and benthic" runs include pelagic and benthic groups, and "Benthic only" runs only include the benthic fraction of the food web. Note that all the groups above the dotted line are considered to be pelagic components and all the groups below the dotted line are considered to be benthic components.

	Codes for model runs in which groups are omitted																				
	Pelagic only							Pelagic and benthic								Benthic only					
Group Code	**OP1**	**OP2**	**OP3**	**OP4**	**OP5**	**OP6**	**OP7**	**OA1**	**OA2**	**OA3**	**OA4**	**OA5**	**OB1**	**OB2**	**OB3**	**OB4**	**OB5**	**OB6**	**OB7**	**OB8**	**OB9**
PL	Y	Y		Y	Y	Y	Y	Y	Y	Y	Y	Y	Y*	Y*	Y*	Y*	Y*	Y*	Y*	Y*	Y*
AF																					
PS			Y	Y	Y	Y	Y		Y	Y	Y	Y									
DF					Y	Y	Y														
PFB							Y					Y									
PAB[+]							Y[+]					Y[+]									
HF																					
ZS				Y	Y	Y	Y		Y	Y	Y	Y									
ZL	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y									
ZLC																					
FP		Y	Y	Y		Y	Y	Y	Y	Y	Y	Y									
FV						Y	Y														
FD								Y	Y	Y	Y	Y			Y			Y	Y	Y	Y
FG											Y									Y	Y
MA								Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
SG										Y	Y	Y				Y	Y	Y	Y	Y	Y
MB											Y					Y		Y		Y	Y
MZ								Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
BG											Y					Y		Y		Y	Y
BF								Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y	Y
BC										Y	Y	Y				Y	Y	Y	Y	Y	Y
BD										Y	Y	Y		Y		Y	Y	Y	Y	Y	Y
OB												Y					Y		Y		Y
AEB												Y					Y		Y		Y
ANB												Y					Y		Y		Y

* A generic water column food group for the benthic feeders that is a forcing function and not a dynamic group.
[+] Bay Model 2 only.

group is present in these runs, but it is only a forcing function in this case). As for the runs using webs produced by aggregating groups, each of the runs using a web produced by omitting groups has a code (listed in Table 5.4). These codes begin with O, the second letter indicates the fraction of the ecosystem considered (as before, P for pelagic only, B for benthic only, and A for benthic and pelagic), and the number represents the relative amount of omission used (the lower the number the more groups that have been omitted from the model web).

5.2.C Altered ecosystem conditions

Some of the runs (Table 5.5) were repeated with nutrients, or fishing pressure, increased fivefold. These runs were chosen to span the range in magnitude of simplification by omission and aggregation. This allows for consideration of the effects of ecosystem change on the relative performance of models with varying trophic complexity.

Table 5.5: List of the trophic simplifications (models) considered under a fivefold increase in nutrient load or fishing pressure. Codes are as in Table 5.3 for models with aggregated groups and in Table 5.4 for models with omitted groups.

Models with aggregated groups	Models with omitted groups
LP2	OP1
LP5	OP2
LA1	OP6
LA3	OA1
LA6	OA4
LA8	OB1
LB4	OB3
LB8	OB6
LB14	OB8

5.2.D Analysis

Summarising the overall effects of model simplification

To summarise the range of system structures encompassed by the simplifications we examine, the number of links and connectance (C) of the system is plotted against the number of groups in each case. C was calculated as given in Putman (1994):

$$C = \frac{L}{N(N-1)} \tag{5.1}$$

where C is connectance, L is the number of links in the web and N is the number of separate "species" in the web (in this case either the original components or the aggregated groups). A number of indices (chlorophyll a, levels of sediment oxygen, denitrification and the biomass, production and consumption of each of the components in the models) are used to judge the relative performance of the models. In each case the runs are compared by considering the absolute relative value of the difference between the averages (over the entire bay for the final four years of each run) of the simplified and standard (full version) runs of the model. Finally, the following measure was taken as an overall indicator of performance:

$$V = \sum_j \frac{\left| I_j^{std} - I_j^{simplif} \right|}{I_j^{std}} \tag{5.2}$$

where I_j is the jth relevant indicator (i.e. Vs calculated for runs containing pelagic components only are based only on pelagic indicators) and "std" and "simplif" indicate the value of the jth indicator for the standard run and simplified run respectively. The simplified model with the smallest value of this overall measure V is considered to have the best overall performance. It is recognised that a very low contribution for a single indicator (Ij) by a run with generally poor performance could better a consistent performance by another run. Fortunately this situation does not arise here. For models that omitted groups, the models that produced the minimum values of V are also the ones that are consistently sound performers (within the top 25%). The relative quality of

each run, as specified by the indicators, is not as consistent for models with aggregated groups as for models with omitted groups. However, the use of V as an overall summary statistic is still acceptable as the "best" run was usually within the top 35% for every indicator.

Summarising the fine scale spatial and temporal effects of model simplification

The output is also considered on a cell-by-cell basis, not just for the bay as a whole. This allows for detection of effects of model simplification on the spatial details of the output.

To judge the effects of model simplification on the fine scale spatial dynamics of the models the relative spatial distributions of each component was tracked over the final four years of each run. The quality of the match at each point is based on the number of boxes for which the distribution in the run using a simplified web differs from the distribution predicted in the standard run. To summarise these results across runs, three broad categories of responses are recognised:

- the spatial distribution of the component matches the spatial distribution in the standard run for the majority of the runs using simplified webs
- there is no match between the spatial distribution of the component in the standard run and any of the runs using simplified webs
- there is only a match between the spatial distribution of the component in the standard run and the runs using simplified webs that have the lowest values for V (as defined above).

A simple comparison of the time series of each component (achieved by overlaying the time series from simplified runs on the time series from the standard run) is used to judge the effects of model simplification on the temporal dynamics of the model.

5.3 Results

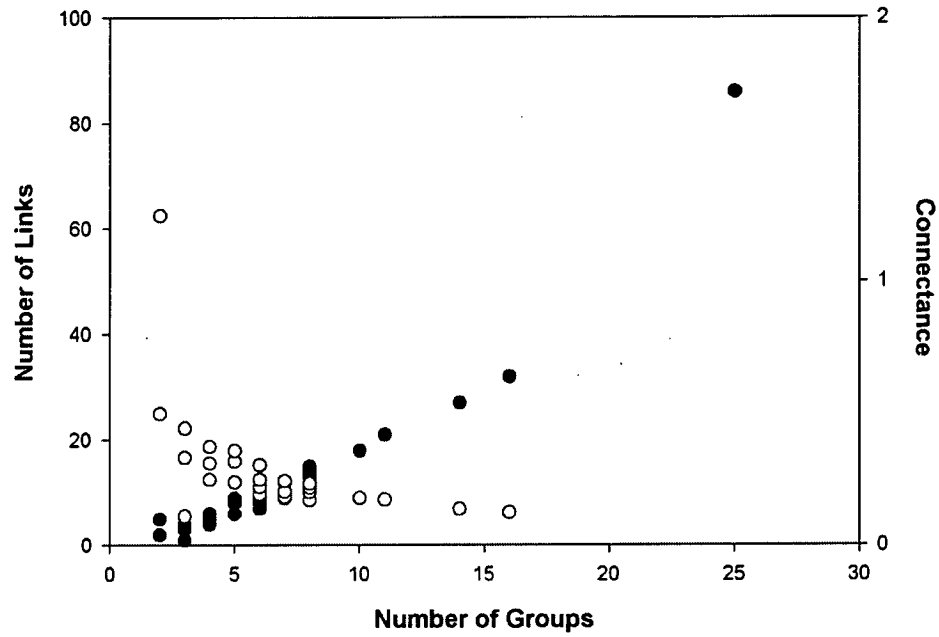
When simplification of the food web is produced by aggregating components there is a clear increase in connectance as the number of nodes (individual components or aggregated groups) is decreased (Figure 5.3). This reflects the marked decrease in the number of links remaining in the web as the number of nodes is reduced (Figure 5.3). Results for simplified food webs produced by omitting groups are similar (Figure 5.4), but the relationships are not as tight. In both cases (omission and aggregation of groups) the small differences in web structure between BM2 and IGBEM (BM2 has an additional pelagic bacteria group) have little effect on the results (Figure 5.3(a) vs. 5.3(b), and Figure 5.4(a) vs. 5.4(b)).

Effects of aggregating groups

In both IGBEM and BM2, a number of the models with aggregated groups that only consider the benthos (the LB models) show trophic self-simplification through the extinction of some functional groups. Some of the simplified versions of BM2 that are the most highly aggregated (runs LB2 – LB4, see Table 5.3 for definitions of the codes) lose the composite "all benthos" component, as does the LB4 run of IGBEM. While no groups go extinct in the less aggregated LB runs of BM2, some groups are lost in IGBEM with the same level of aggregation. The LB8, LB9 and LB12 runs of IGBEM all suffer some form of trophic self-simplification. All of these runs have an aggregated demersal fish group, microphytobenthos and infauna and epifauna groups that are aggregated to slightly different degrees. In LB8 all but the microphytobenthos drop to negligible levels of biomass; LB9 loses the lumped "all infauna" group; and LB12 loses the "large infauna" aggregated group. It is noteworthy that these models undergo trophic self-simplification in IGBEM when they do not in BM2 and that even other versions of IGBEM with very similar levels of aggregation (e.g. LB10 and LB11) do

Figure 5.3: Plot of connectance (C) (open circles) and the number of links (solid black circles) in the simplified food webs produced by aggregating components, against the number of groups (individual functional groups or aggregated groups) in the webs.

(a) Bay Model 2 (BM2)



(b) for the Integrated Bay Ecosystem Model (IGBEM)

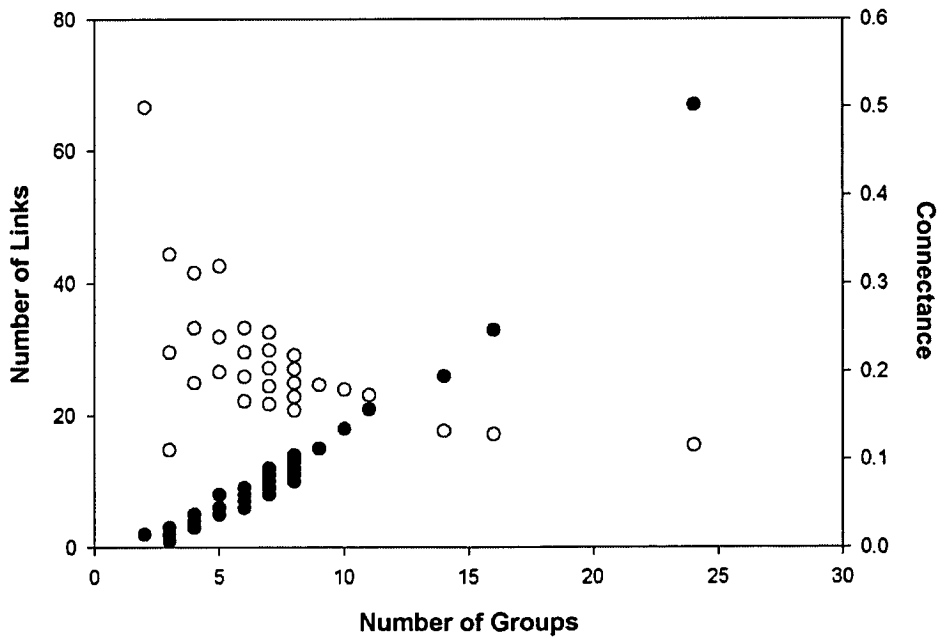
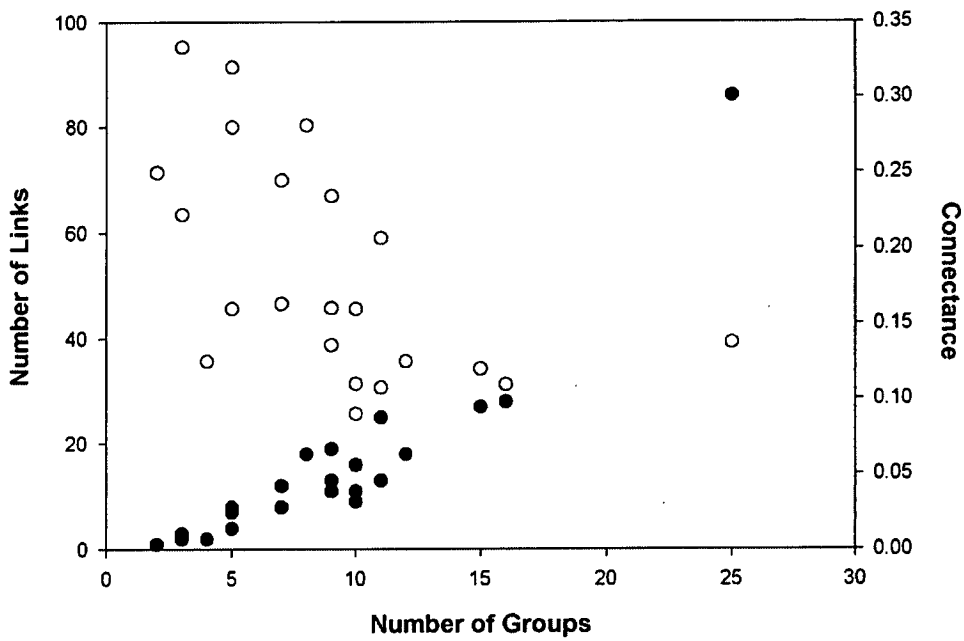
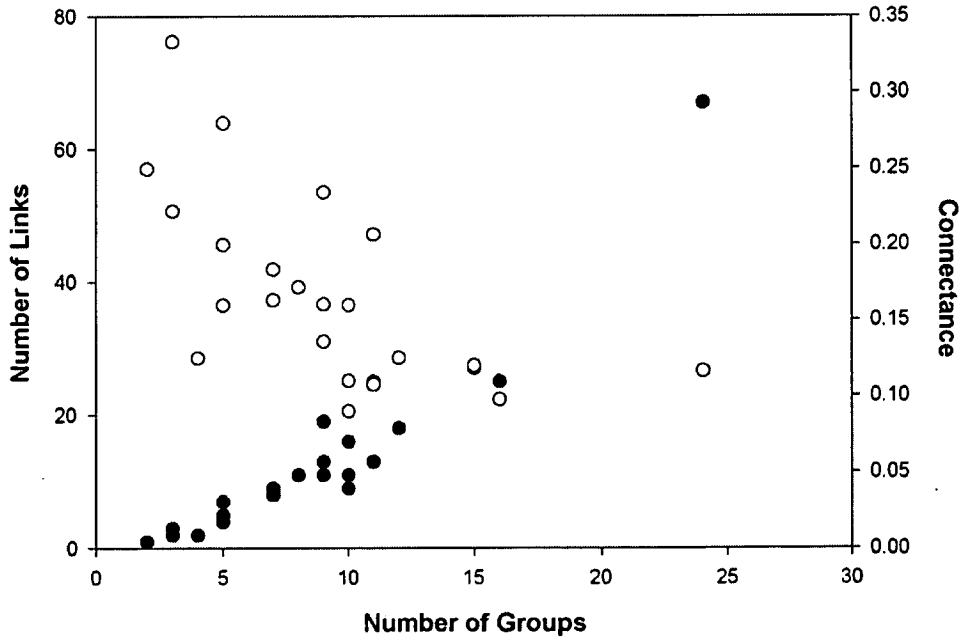


Figure 5.4: Plot of connectance (C) (open circles) and the number of links (solid black circles) in the simplified food webs, produced by omitting components, against the number of functional groups in the webs.

(a) Bay Model 2 (BM2)



(b) the Integrated Bay Ecosystem Model (IGBEM)



not self-simplify in this way. Two of the runs that use aggregated food webs that span pelagic and benthic components also predict the extinction of some groups. In the LA8 run of BM2 the benthic consumers, except the "mobile epifauna", decline to negligible levels, and the LA9 run of IGBEM loses the diatoms and the aggregated group "small zooplankton". There are also a number of versions of IGBEM with aggregated groups where the system approaches numerical instability (these are LA3 and all of the LB runs that include the aggregated groups "macrophytes" or "all phytobenthos").

It is possible to compare indices across the models despite extinction of some groups and potential instabilities. A majority of the indices show no clear patterns when the absolute relative differences in the values for the simplified and standard runs are plotted against the number of groups in the run (Figure 5.5). Only denitrification shows a clear effect of aggregating groups, and that is that the upper bound of the absolute relative difference in predicted denitrification in the simplified *vs* full models increases as more groups are aggregated (Figure 5.5). None of the indicators shows any clear patterns when plotted against connectance for either BM2 or IGBEM.

A final way of considering the baywide averages for the indices is to evaluate them in relation to the subwebs that are preserved in each run, that is to explicitly consider the results per run. Considering the results of each run in this way, it is clear that the behaviour of models with aggregated groups are frequently very different to those of the full versions without aggregation. Deviations from the non-aggregated models of the predicted values of the various indicators are often greater for versions of BM2 and IGBEM with aggregated groups than for versions with omitted groups (Table 5.6). The amount of deviation has a non-linear relationship with the level of aggregation used. For each indicator there is usually one or more runs with intermediate levels of aggregation for which the amount of deviation is smaller than for other runs with higher or lower levels of aggregation (e.g. chlorophyll a in the LP runs, Figure 5.6). This

Figure 5.5: Plots of the absolute relative differences in the predicted values of indices between the simplified (with aggregated trophic groups) and full versions of the models in relation to the number of groups (individual functional groups or aggregates) included in the models. (Note: the larger the number of components the lower the degree of aggregation.) The results for Bay Model 2 (BM2) are represented by open circles and those for the Integrated Generic Bay Ecosystem (IGBEM) by solid black circles. The indices are: (a) chlorophyll a in the water column, (b) chlorophyll a on the sediments, (c) denitrification, (d) concentration of oxygen in the sediments, (e) water column primary production, (f) total consumption in the water column, (g) benthic primary production, (h) total benthic consumption, (i) biomass of macrophytes, (j) biomass of zooplankton, (k) biomass of benthos, and (l) biomass of fish.

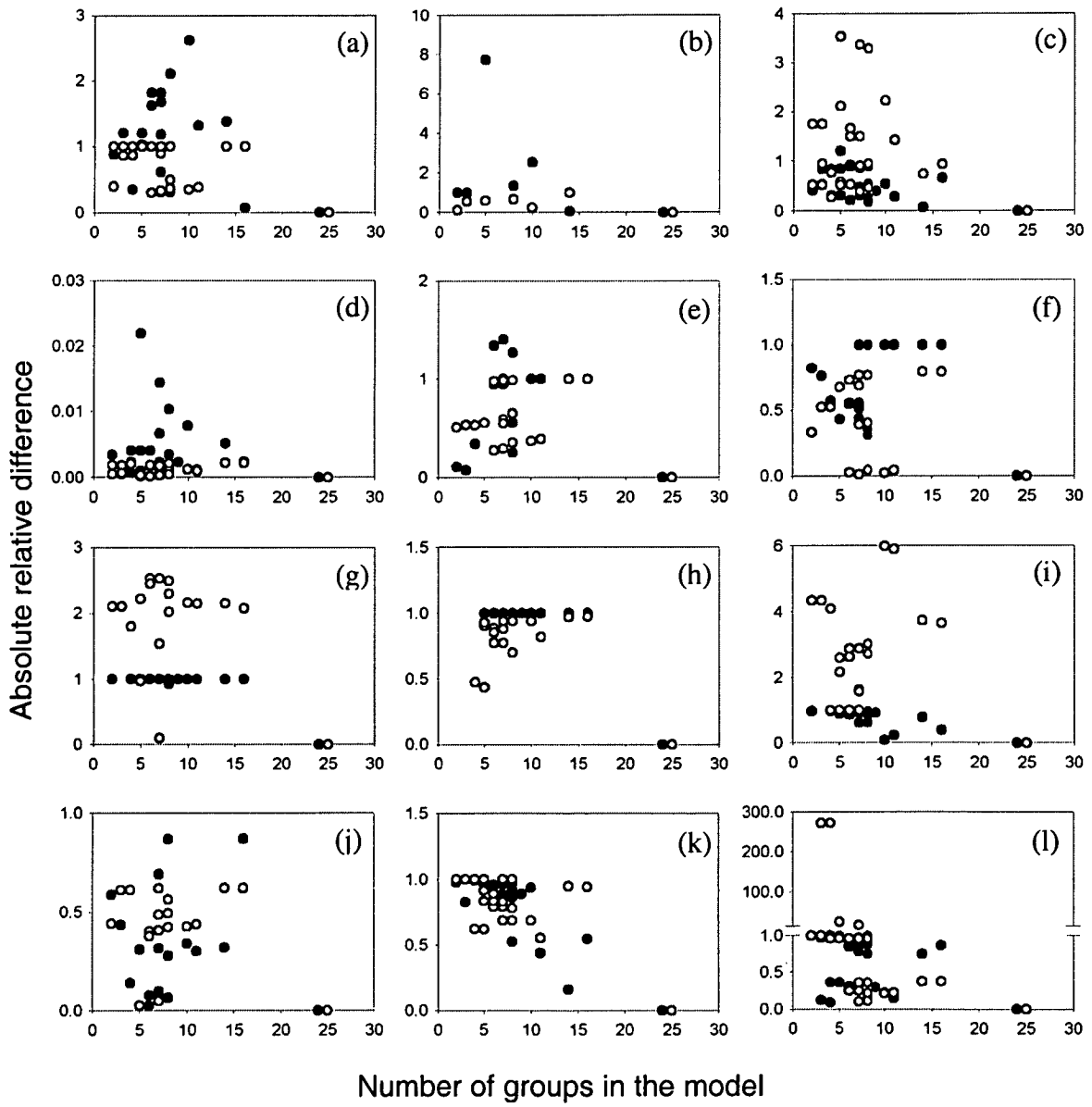


Table 5.6: Comparison of the magnitude of average relative deviation from the full models of the indices from runs produced by aggregation and omission of groups for Bay Model 2 (BM2) and the Integrated Bay Ecosystem Model (IGBEM). Values in the table are the average ratio of the deviation for models with aggregated groups: the deviation of models with omitted groups with the same degree of simplification.

Index	BM2	IGBEM
Biomass of fish	59.3	1.0
Biomass of macrophytes	7.7	2.2
Biomass of zooplankton	0.8	0.9
Biomass of benthos	0.5	0.5
Chlorophyll a	0.5	1.4
Consumption (water column)	1.0	1.2
Consumption (sediment)	1.5	2.2
Denitrification	1.2	1.8
Primary Production (water column)	2.3	1.3
Primary Production (sediment)	3.7	2.0
Sediment Oxygen	0.3	1.3

general pattern is also evident in the overall *V* statistics for models with aggregated groups (Table 5.7). Consideration of the structure of the food web in each of the models with aggregated groups (Table 5.3) that have the lowest *V* values (Table 5.7) suggests that retaining broad trophic level and size structure is necessary for reasonable model performance.

Considering fine-scale spatial and temporal resolution rather than baywide averages, there are still strong effects of aggregating groups. Overall, there are relatively few processes with a fairly consistent distribution over all the runs and these are driven largely by production and consumption by the fish (Table 5.8). There are many more components and processes for which the relative spatial distributions in the runs with aggregated groups do not match the relative spatial distribution of the non-aggregated model (Table 5.8). Many of these processes and measures are associated with bacteria. A notable exception is the biomass of zooplankton. None of the runs with aggregated groups predict a relative distribution for this measure which matched the relative distribution in the full versions of BM2 or IGBEM. In comparison to the number of components and processes that do not match the relative distribution of the standard run, a similar number have relative spatial distributions that only match those of the standard

run for the models with aggregated groups that have the lowest V values (e.g. LA5 for BM2). For many of the benthic components and processes in this category there is a discernible degradation between the match of the relative spatial distribution in the runs with aggregated groups and the distribution in the full version as the amount of aggregation is increased. Generally there is a sharp transition in performance at the point when the aggregation of groups removes the size structuring of the benthic primary producers and the distinction between infauna and epifauna.

Table 5.7: Overall performance indicators (V) for the simplified versions of Bay Model 2 (BM2) and the Integrated Bay Ecosystem Model (IGBEM), when simplification was by aggregating trophic groups. The lower the value of V the better the overall performance of the run relative to the full model.

	Pelagic Only		Pelagic and Benthic		Benthic Only	
Run	**BM2**	**IGBEM**	**BM2**	**IGBEM**	**BM2**	**IGBEM**
LP1	1.68	2.40				
LP2	274.56	2.60				
LP3	275.04	1.48				
LP4	3.08	3.54				
LP5	1.25	4.25				
LP6	1.27	4.24				
LP7	3.74	4.55				
LP8	3.68	2.08				
LA1			35.21	15.25		
LA2			24.06	14.99		
LA3			24.91	7.04		
LA4			10.71	8.42		
LA5			9.44	12.34		
LA6			11.47	10.30		
LA7			11.18	7.68		
LA8			11.20	6.53		
LA9			11.31	6.93		
LB1					3.53	3.37
LB2					4.53	4.85
LB3					4.76	3.40
LB4					5.73	3.67
LB5					4.95	4.85
LB6					4.75	3.67
LB7					3.34	4.55
LB8					5.13	3.48
LB9					4.29	4.43
LB10					3.37	3.59
LB11					5.03	3.47
LB12					4.22	4.67
LB13					4.42	3.21
LB14					5.03	4.22
LB15					4.58	4.23
LB16					3.91	3.47

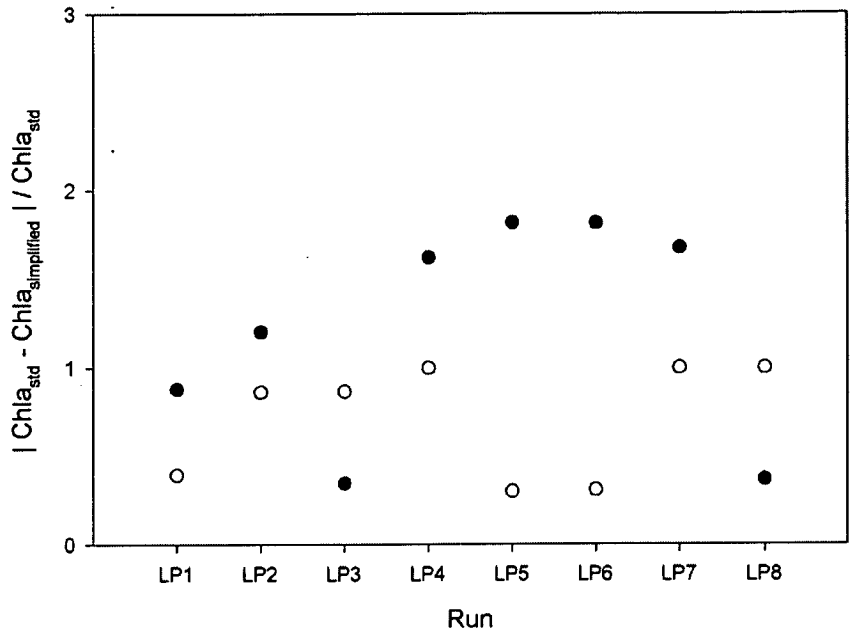


Figure 5.6: Relative differences between the chlorophyll a concentrations provided by the simplified (with aggregated trophic groups) and full (std) models. The results for Bay Model 2 (BM2) are represented by open circles and those for the Integrated Generic Bay Ecosystem (IGBEM) by solid black circles.

Table 5.8: Categories of the effects of aggregating groups on the relative spatial distribution of the constituent components, and associated processes, in Bay Model 2 (BM2) and the Integrated Generic Bay Ecosystem Model (IGBEM). Codes are as in Table 5.1, and the standard distribution is the spatial distribution in the full model.

Match standard distribution for most runs	No match with standard distribution	Match standard distribution only for runs with lowest *V* values (see Table 5.7)
• Total water column secondary production and consumption • Total production and consumption by pelagic, piscivorous and demersal fish • Total denitrification (BM2 only)	• Biomass of zooplankton • Biomass of pelagic bacteria • Biomass of sediment bacteria • Total production and consumption by pelagic bacteria • Total production and consumption by sediment bacteria • Biomass of phytobenthos (BM2 only) • Biomass of epifauna (BM2 only) • Total benthic primary production (IGBEM only)	• Chlorophyll a • Total water column primary production • Total benthic secondary production and consumption[T] • Biomass of infauna[T] • Total biomass of the benthos[T] • Total biomass of fish[T] • Biomass of phytobenthos (IGBEM only)[T] • Biomass of epifauna (IGBEM only) • Total denitrification (IGBEM only)

[T] Threshold effect: with a decrease in aggregation there is a sharp transition between displaying very poor relative spatial distributions and approaching the relative spatial distribution of the full model.

The temporal dynamics displayed by the models with aggregated groups are more often like each other than the corresponding components in the standard run of BM2 or IGBEM. For example, for BM2 the time series for "large zooplankton" in LP2 is similar to the time series produced by adding the time series for "small zooplankton" and "large zooplankton" in LA6, but is markedly different from the time series produced by adding the time series for all the zooplankton groups in the standard run (Figure 5.7). The general forms of the dynamics of aggregated and non-aggregated models is more similar when the amount of aggregation is lower, though even then critical details such as bloom peaks are not predicted accurately in versions with aggregated groups (Figure 5.8). If the degree of aggregation is high then there is little, if any, resemblance between the temporal dynamics of the standard and simplified runs for a large number of the trophic groups, particularly the fish, benthos and macrophytes.

Effects of omitting groups

BM2 demonstrates trophic self-simplification, in which functional groups went extinct in the run, in 5 cases. In OA2 (see Table 5.4 for definitions of the codes), macroalgae was lost from the system, while in OB4, OB6, OB8 and OB9 the biomass of the benthic deposit feeders fell to negligible levels. In contrast, for IGBEM, macroalgae and the benthic deposit feeders show a reduced spatial distribution for some of the runs, but no component is entirely lost from the system.

There are a number of runs where the system becomes susceptible to the effects of increased short-term nutrient loading (e.g. flooding of the Yarra River, which is a key point source of inputs in the model). As a result the system exhibits extreme behaviours (such as high amplitude oscillations in some components) or approaches numerical instability. This is more common in IGBEM than in BM2. In BM2 only OA5 exhibits this problem, while for IGBEM the runs OB2 – OB9 (inclusive) also display this behaviour.

Figure 5.7: Comparison of the temporal dynamics of "large zooplankton" in LP2, the time series produced by adding the time series for "small zooplankton" and "large zooplankton" in LA6 and the time series produced by adding the time series for all the zooplankton groups in the standard (full) version of Bay Model 2 (BM2). The codes for the runs simplified by aggregating groups (LP2, LA6) are given in Table 5.3 and all time series come from the same cell of the model (close to the mouth of the modelled bay).

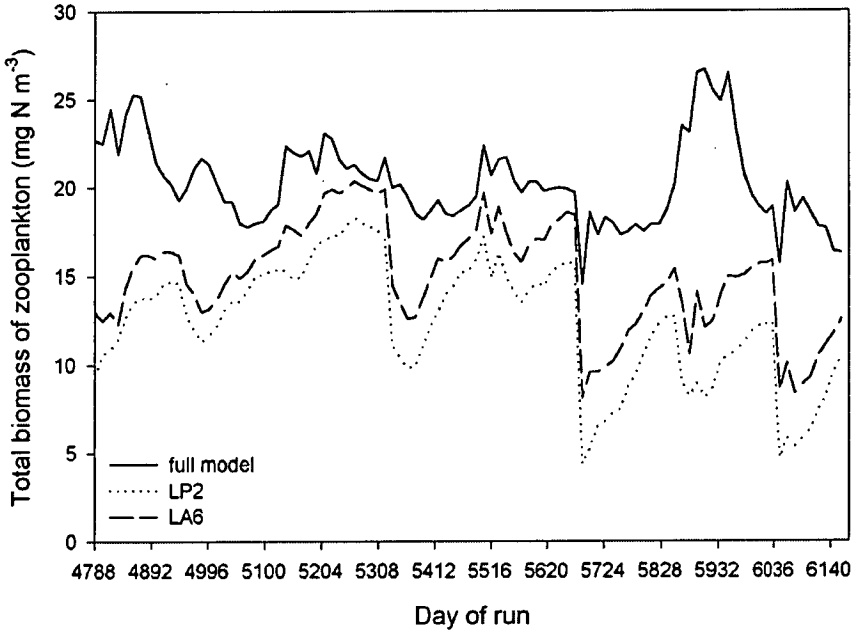
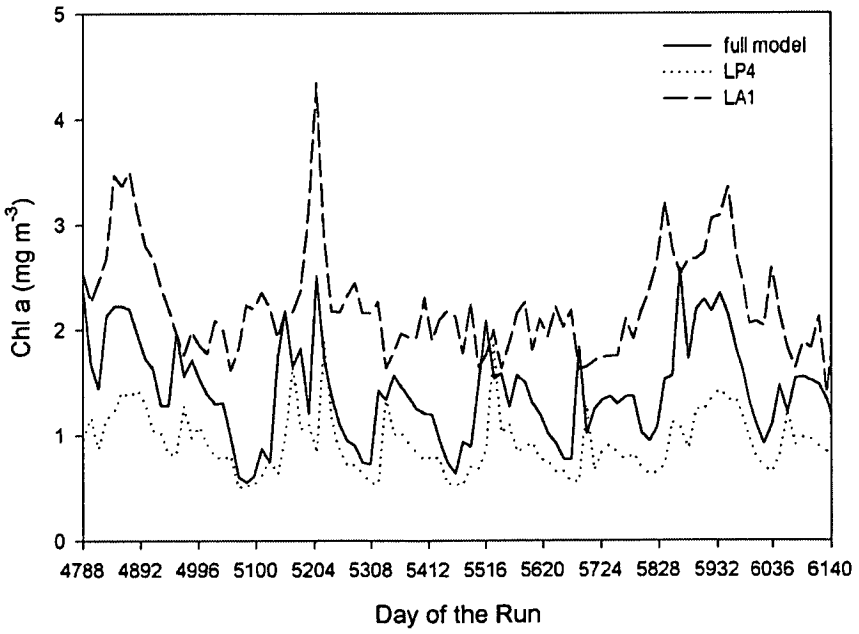


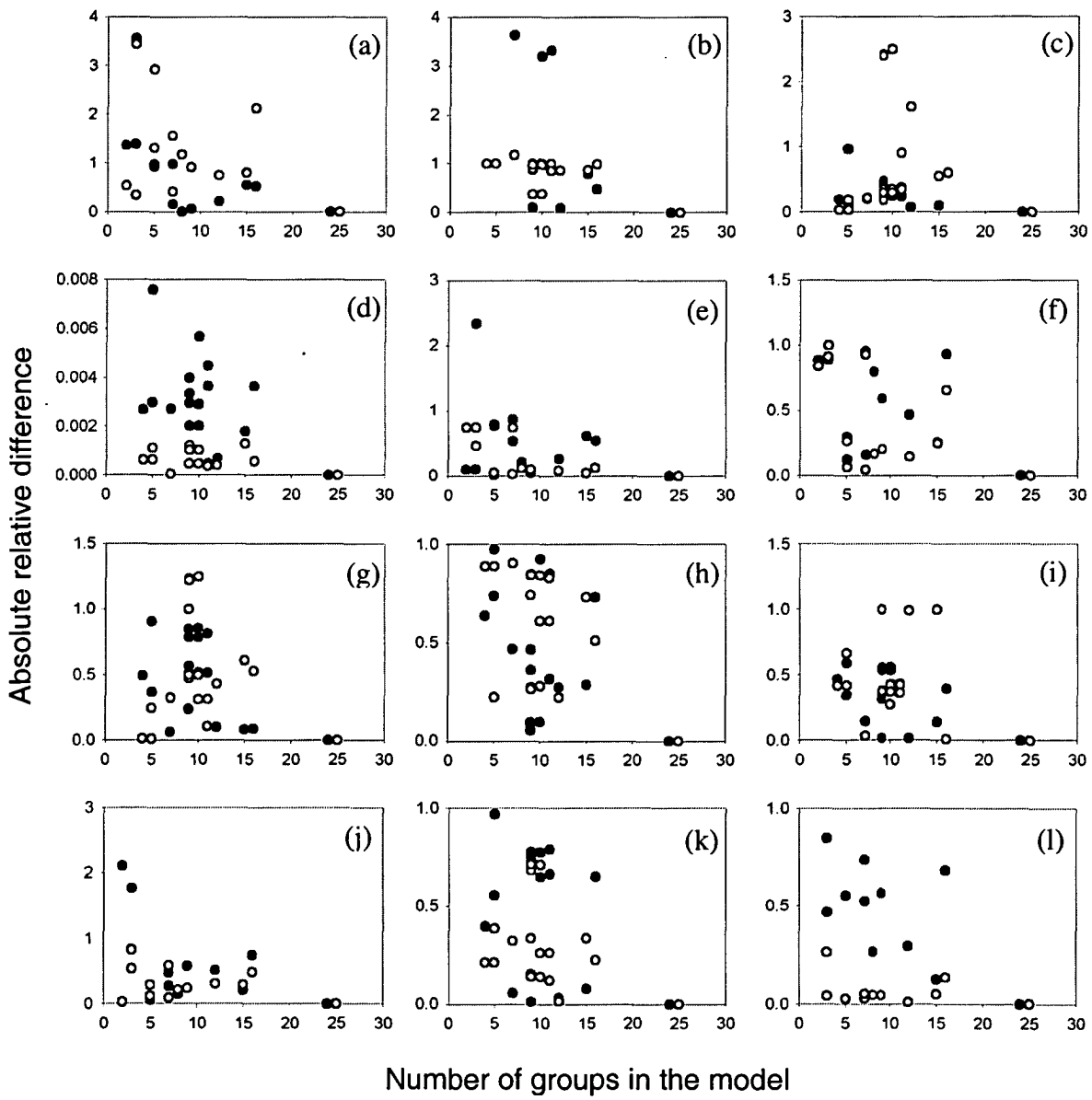
Figure 5.8: Comparison of the temporal dynamics of chlorophyll a (Chl a) in one cell (covering an input point from a sewage treatment plant) of the standard (full) model and versions of Bay Model 2 with aggregated groups. For clarity, only a selection of the simplified models are displayed, but all the simplified models produced levels of Chl a between the extremes presented here.



Despite the extinction of some groups and instabilities, it is possible to compare indices across the models. When the absolute relative differences between the simplified versions (with omitted groups) and the standard (full) model are plotted against the number of groups, there are some clear results and these patterns are stronger for IGBEM than BM2 (Figure 5.9). For BM2 there is no clear overall pattern of the effect of omitting groups on the levels of oxygen (Figure 5.9d) or chlorophyll in the sediment (Figure 5.9b), or the predicted average biomass of planktivorous fish (Figure 5.9l) or macroalgae (Figure 5.9i). There is a clear pattern for the rest of the indices for BM2, but it is not usually as marked as that shown by IGBEM. The general pattern of the effect of omitting groups is that the upper bound on the absolute relative difference between the simplified and full versions of the model increases as more groups are omitted (Figure 5.9). The pattern is not equally strong across all indices, even in IGBEM, and is clearest for water column variables, such as chlorophyll a (Figure 5.9a), the biomass of large omnivorous zooplankton (Figure 5.9j), and denitrification in the sediments (Figure 5.9c). This relationship, between the absolute relative difference between the models and the number of groups omitted, is less evident for the biomass of the benthic groups, for example benthic filter feeders (Figure 5.9k). In contrast to the consistent patterns between performance of reduced models and the number of groups they contain, there is no clear relationship between any of the indices and connectance for either BM2 or IGBEM.

Considering the results of each run individually shows that there are crucial links that have to be included if the behaviour of the simplified models is to approach that of the full version of BM2 or IGBEM. This is indicated clearly by estimates for primary production and consumption (Figures 5.10 and 5.11). If few groups are included in the simplified web then the productivity estimates from simplified models usually diverge from equivalent estimates from the full model by as much as 50-85%. The effect is

Figure 5.9: Plot of the absolute relative differences in the predicted values of indices between the simplified (with omitted trophic groups) and full versions of the models in relation to the number of groups included in the models. (Note: the larger the number of components the fewer groups that have been omitted.) The results for Bay Model 2 (BM2) are represented by open circles and those for the Integrated Generic Bay Ecosystem (IGBEM) by solid black circles. The indices are: (a) chlorophyll a in the water column, (b) chlorophyll a on the sediments, (c) denitrification, (d) concentration of oxygen in the sediments, (e) water column primary production, (f) total consumption in the water column, (g) benthic primary production, (h) total benthic consumption, (i) biomass of macroalgae, (j) biomass of large omnivorous zooplankton, (k) biomass of benthic filter feeders, and (l) biomass of planktivorous fish.



particularly severe in the "benthic only" runs, where benthic primary production is consistently more than 35% from the value given by the full model, except for some of the simplest of the BM2 cases (OB1 and OB3) where it is within 2% of the standard estimate (Figure 5.10). The results for consumption (Figure 5.11) are largely similar to those for production. Runs with only a few groups in them produce estimates of consumption that deviate most from the standard estimate (by as much as 90%). Notably the consumption estimate from the run with the fewest omitted groups usually also performs poorly (as poorly as the most simplified runs). This suggests that the inclusion of bacteria may not be appropriate in simplified webs.

Consideration of food web structure (Table 5.4) in each of the runs with the lowest values of the *V* statistic (Table 5.9) indicates that some representation of size structure is required in simplified food webs and that benthic subwebs may need to be more highly resolved than pelagic subwebs. Further, the results suggest that representing many of the microfaunal functional groups may not be necessary.

As might be expected given the overall responses of the model to omitting groups, the fine scale output of the models is also affected by omitting groups. As occurs in the overall indices, not all components and processes in the models are affected to the same degree by the omission of groups. Generally, the relative spatial distribution of some microfauna (meiobenthos and the pelagic bacteria) does not match the standard case for any of the simplified runs in which they are included (Table 5.10). In contrast, the distribution of fish, picoplankton and total water column production is virtually identical to that of the full model for all runs of the simplified versions of BM2 and IGBEM (Table 5.10). There are also a couple of components (macroalgae in BM2 and anaerobic bacteria in IGBEM) for which the relative spatial distributions in the simplified and standard runs are close matches in only one of the two models. It is not surprising that the relative spatial distributions of the fish are close matches in all the

Figure 5.10: Absolute relative differences between estimates of primary production between models with omitted groups (simplif) and the full (std) model. (a) Water column primary production, and (b) benthic primary production. The results for Bay Model 2 (BM2) are represented by open circles and those for the Integrated Generic Bay Ecosystem (IGBEM) by solid black circles.

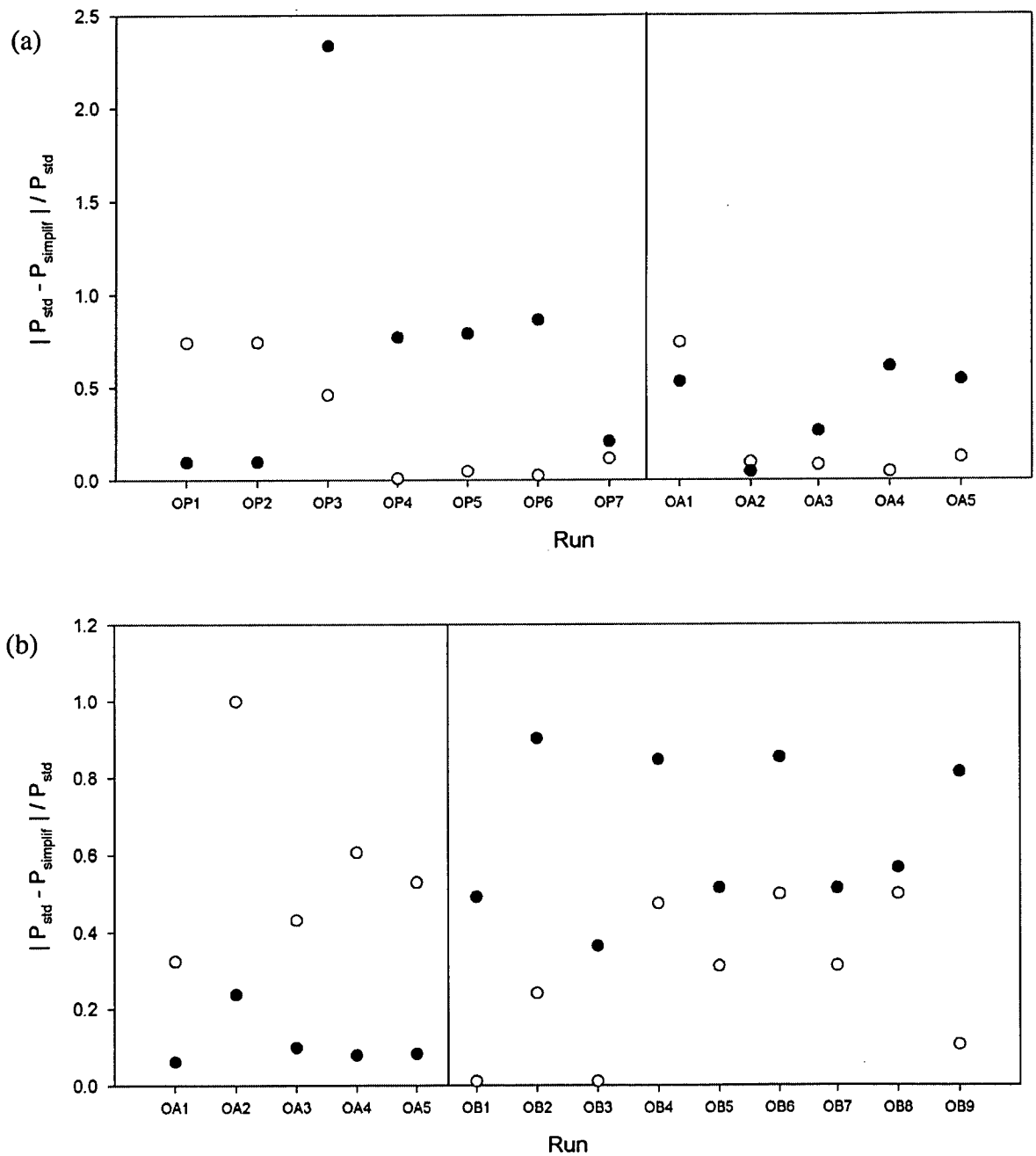


Figure 5.11: Absolute relative differences between estimates of consumption between models with omitted groups (simplif) and the full (std) model. (a) Water column consumption, and (b) benthic consumption. The results for Bay Model 2 (BM2) are represented by open circles and those for the Integrated Generic Bay Ecosystem (IGBEM) by solid black circles.

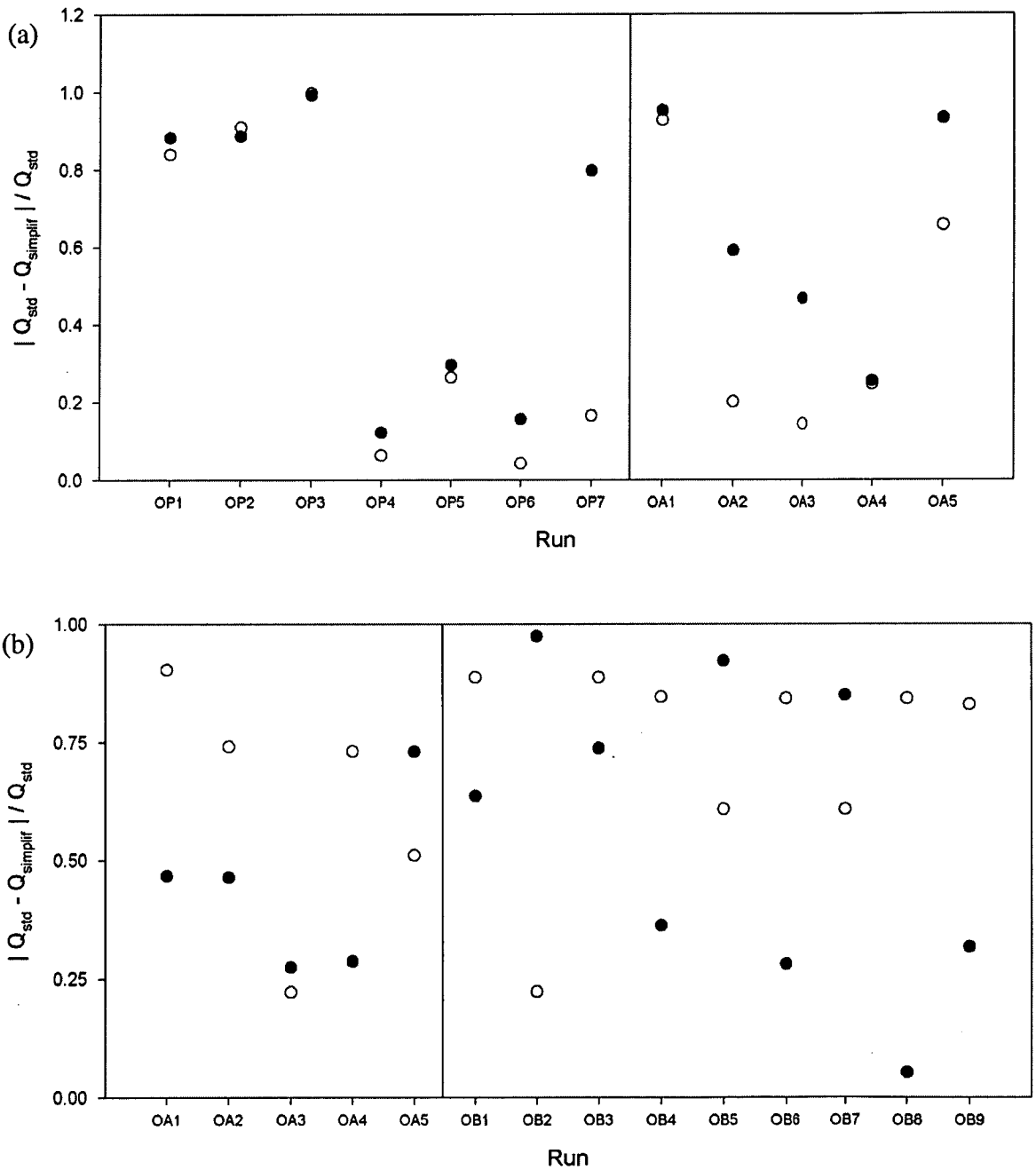


Table 5.9: Overall performance indicators (*V*) for runs of Bay Model 2 (BM2) and the Integrated Bay Ecosystem Model (IGBEM), with groups omitted from the models. The lower the value of *V* the better the overall performance of the run relative to the full model.

	Pelagic Only		Pelagic and Benthic		Benthic Only	
Run	**BM2**	**IGBEM**	**BM2**	**IGBEM**	**BM2**	**IGBEM**
OP1	3.00	4.45				
OP2	3.49	4.61				
OP3	6.98	8.57				
OP4	1.62	2.47				
OP5	3.82	2.07				
OP6	1.83	3.00				
OP7	1.92	1.42				
OA1			7.63	7.22		
OA2			6.87	3.20		
OA3			6.40	2.45		
OA4			6.81	3.37		
OA5			14.58	6.69		
OB1					2.57	3.89
OB2					2.71	6.26
OB3					2.58	3.41
OB4					3.09	3.92
OB5					2.96	6.20
OB6					2.54	3.81
OB7					2.95	6.49
OB8					2.54	3.22
OB9					3.20	3.72

Table 5.10: Categories of the effect of omitting groups on the relative spatial distribution of the constituent components, and associated processes, in Bay Model 2 (BM2) and the Integrated Generic Bay Ecosystem Model (IGBEM). Codes as are as in Table 5.1, and the standard distribution is the spatial distribution in the full model.

Match standard distribution for nearly all runs	**No match with standard distribution**	**Match standard distribution only for runs with lowest *V* values (see Table 5.9)**
• FD*, FG*, FP*, FV*, PS, • Total water column primary production, • Total production and consumption by FD and FV, • ANB (IGBEM only), • Macroalgae (BM2 only)	• OB, PB (PAB and PFB for BM2), • Total production and consumption by pelagic bacteria, • DF (BM2 only)	• AEB, BC, BD, BF, BG, MB, MZ, PL, SG, ZL, ZS, Chlorophyll a, • Total benthic primary production, • Total benthic secondary production and consumption, • Total water column secondary production and consumption, • Total denitrification, • Total production and consumption by benthic bacteria, • Total production and consumption by FG and FP, • ANB (BM2 only)

* A fixed migration matrix gives the spatial distribution of the biomass of these groups. However, the distribution of production and consumption by these groups is not fixed as that depends on the local density of their food groups.

runs because a migration matrix fixes their distribution. However, it is noteworthy that the relative spatial distributions for the picophytoplankton, and the macroalgae in BM2 are close matches in all the runs. Nevertheless, only a minority of the components in the runs with omitted groups have relative spatial distributions that either match the distribution in the full model closely or not at all. The relative spatial distribution of the majority of components and processes only approaches that of the standard run for those models with omitted groups that are identified by the overall indicator (V) as being close to the standard output (e.g. OA3).

The temporal dynamics of the models with omitted groups indicated that the turnover time of a component is one of the central factors determining the degree to which omitting groups degrades the model performance. The slower growing components usually show little change in temporal patterns as a result of omission (e.g. biomass of the epifaunal carnivores, Figure 5.12), while the greatest changes are associated with groups with rapid dynamics (e.g. diatoms, Figure 5.13).

Influence of changes to the ecosystem conditions on the effects of simplifying models

Increasing nutrient load or fishing pressure does not change the general pattern of effects of simplification based on baywide measures reported above, but there are some quantitative differences. The upper bound of the difference between the simplified runs and the full models declines as the total number of groups in the models increased. As for the results under baseline conditions, this pattern is stronger for IGBEM than for BM2. Again, there is no relationship between the differences of the simplified and standard runs and connectance.

In contrast to the baywide results, the quality of the matches of the relative spatial distributions of the simplified and full models changes substantially for some of the groups and processes when ecosystem conditions are altered. Within models that have either omitted or aggregated groups, the changes tend to be the same whether it is

Figure 5.12: Comparison of the temporal dynamics of epifaunal predators (MZ) in one cell (offshore from a sewage treatment plant) of the full Integrated Generic Bay Ecosystem Model and versions with omitted groups. For clarity, only a selection of the runs has been displayed, but all the runs produced biomasses of MZ between the extremes presented here.

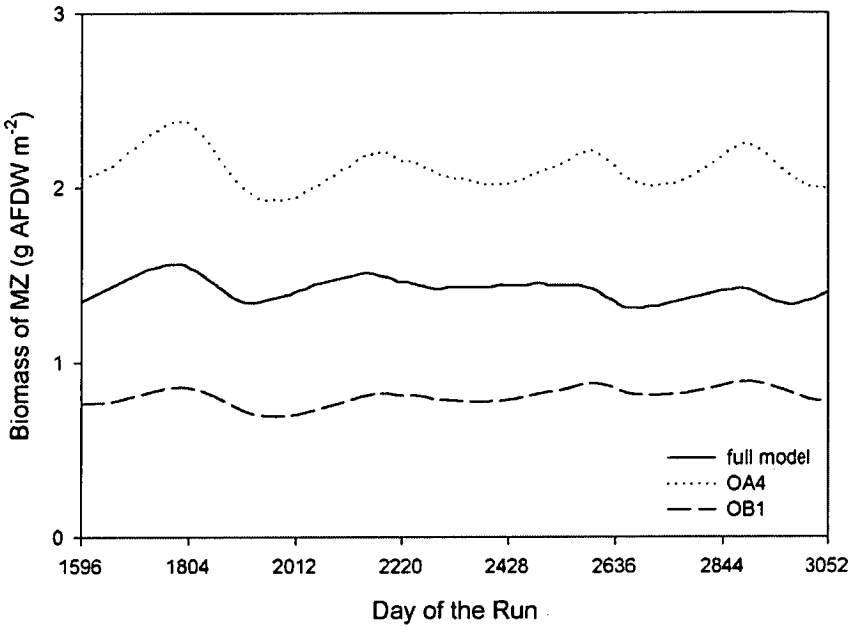
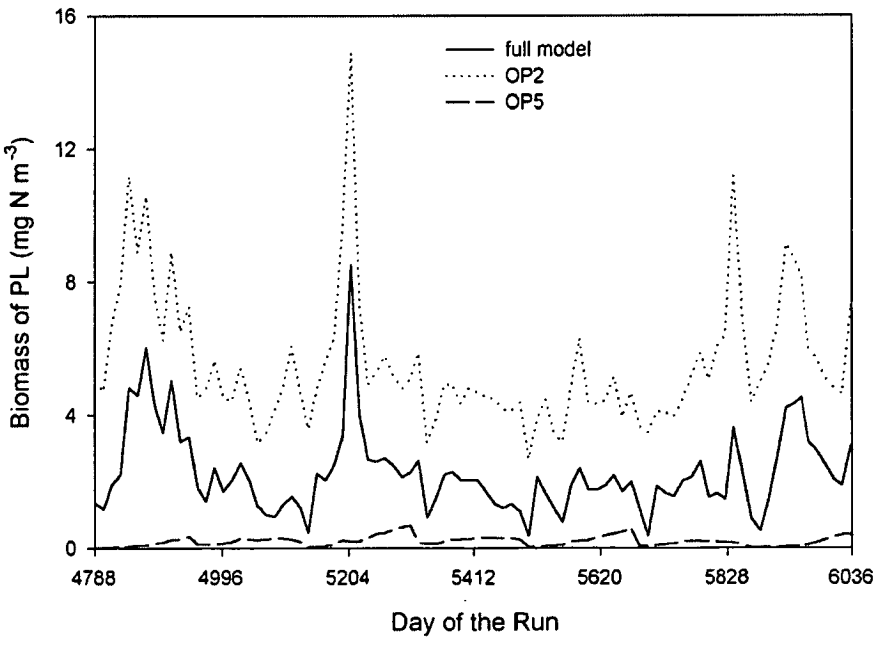


Figure 5.13: Comparison of the temporal dynamics of biomass of diatoms (PL) in one cell (covering an input point from a sewage treatment plant) of the full Bay Model 2 model and versions with omitted groups. For clarity, only a selection of the runs has been displayed, but all the runs produced biomasses of PL between the extremes presented here.



fishing pressure or nutrient loading that changes. However, comparing the changes across models that use different forms of simplification, it is clear that the direction of change is often similar, but the groups and processes affected are different for models that aggregate groups (Table 5.11) and models that omit groups (Table 5.12). The effects of aggregating groups on relative spatial distributions does not change with changing ecosystem conditions for many groups and processes. The majority of the groups and processes for which the effects of aggregation on spatial distributions do change with changing ecosystem conditions move from occasionally matching the distribution in the full model to never matching it (Table 5.11). A similar pattern of change in the results occurs for models with omitted groups when ecosystem conditions are altered. The majority of the components that only show occasional agreement with the full version under baseline conditions now show no agreement (Table 5.12). However, the match for denitrification, benthic primary production and the production and consumption by planktivorous and herbivorous fish improve with altered ecosystem conditions, and many of the components that display relatively consistent spatial distributions across all of the models with omitted groups under baseline conditions continued to do so (Table 5.12).

The same temporal patterns of behaviour, in the simplified models relative to the full model, hold under changed conditions, except that the deviations from the standard run are more exaggerated (e.g. diatoms, Figure 5.14). This is due to the higher levels of resources available to primary producers, or lower predation pressure on the fish prey groups, under the new conditions. These deviations arise when groups are either aggregated or omitted, but are much worse in the former. There are a few cases in the models with aggregated groups where the effects of changing ecosystem conditions are opposite to those predicted by the full model. For example, the overall behaviour of the "macrophyte" group more closely resembles the behaviour of the seagrass in the full

Table 5.11: The effects of model simplification by aggregation on the relative spatial distribution of the constituent components, and associated processes, in Bay Model 2 (BM2) and the Integrated Generic Bay Ecosystem Model (IGBEM) when the nutrient load (x5) or fishing pressure (Fx5) is increased to five times that of the "baseline" conditions. Codes are as in Table 5.1, and the standard distribution is the spatial distribution in the full model under the same nutrient load and fishing pressure.

Match standard distribution for most runs		**Never match standard distribution**		**Occasionally match standard distribution**	
Fx5	**x5**	**Fx5**	**x5**	**Fx5**	**x5**
• Total biomass of fish • Total denitrification • Total production and consumption by pelagic, piscivorous and demersal fish	• Total biomass of fish • Total denitrification • Total consumption by pelagic, piscivorous and demersal fish	• Biomass of epifauna • Chlorophyll a • Biomass of phytobenthos • Total benthic primary production	• Biomass of epifauna • Chlorophyll a • Biomass of phytobenthos • Total biomass of benthos • Total water column primary production • Total benthic primary production	• Biomass of zooplankton • Biomass of infauna • Total biomass of benthos • Total water column primary production, • Total benthic secondary production and consumption • Total water column secondary production and consumption	• Biomass of zooplankton • Biomass of infauna • Total production by pelagic, piscivorous and demersal fish • Total benthic secondary production and consumption • Total water column secondary production and consumption

Table 5.12: The effects of omitting groups on the relative spatial distribution of the constituent components, and associated processes, in Bay Model 2 (BM2) and the Integrated Generic Bay Ecosystem Model (IGBEM) when the nutrient load (x5) or fishing pressure (Fx5) is increased to five times that of the "baseline" conditions. Codes are as in Table 5.1, and the standard distribution is the spatial distribution in the full model under the same nutrient load and fishing pressure.

Match standard distribution for most runs		**Never match standard distribution**		**Occasionally match standard distribution**	
Fx5	**x5**	**Fx5**	**x5**	**Fx5**	**x5**
• BG, FD, FG, FP, FV, MA, SG, ZL • Total denitrification • Total production and consumption by FD, FG, FP and FV	• BG, FD, FG, FP, FV, MA • Total benthic primary production • Total denitrification • Total production and consumption by FD, FG, FP and FV	• BC, BD, BF, DF, MB, MZ, PS, ZS • Total water column primary production • Total water column secondary production and consumption • Total benthic secondary production and consumption	• BC, BD, BF, DF, MB, PS, SG, ZS • Total water column primary production • Total water column secondary production and consumption • Total benthic secondary production and consumption	• PL, • Chlorophyll a	• PL, MZ, ZL, • Chlorophyll a

Table 5.13: Predicted change in biomass (average biomass when nutrient loads x5 / average biomass under baseline conditions) of macrophytes for standard (full) model and versions of Bay Model 2 with aggregated groups.

	Run							
	Standard	LA1	LA3	LA6	LA8	LB4	LB8	LB14
Change in Biomass	1.62	0.09	0.79	0.44	0.97	0.51	0.46	0.15

model than the macroalgae. Consequently, when nutrients rise the "macrophyte" group is lost from the system in the models with aggregated groups, while the biomass of macrophytes (the sum of the biomasses of macroalgae and seagrass) persists and even rises in the standard form of BM2 (Table 5.13).

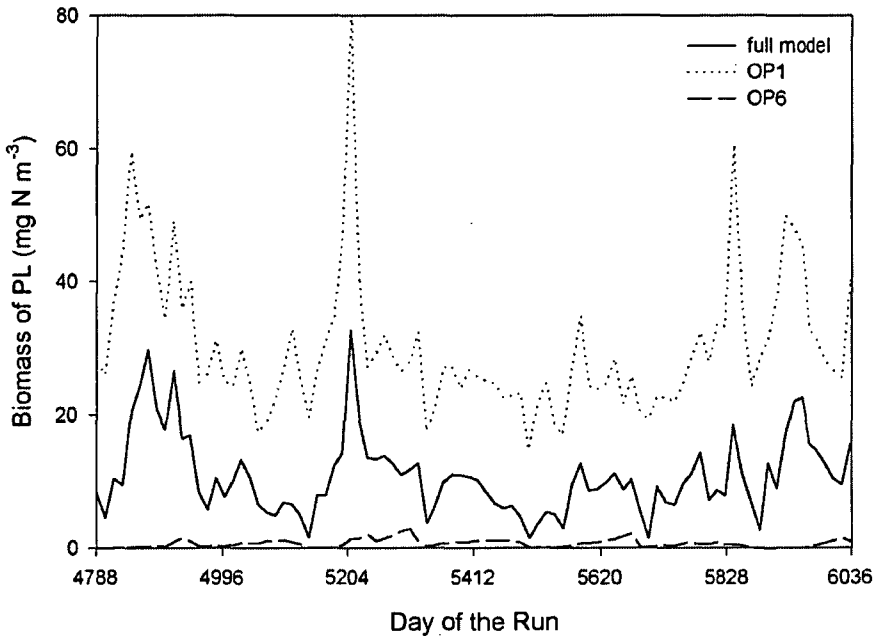
5.4 Discussion

It is possible to make a number of generalisations from the relative performance of the various kinds of simplified models. First, groups with the fastest dynamics often show the greatest effects of reduced model complexity (e.g. consider the temporal dynamics of the various components of the models). This is due to the greater ability of groups with fast dynamics to respond to changes in ambient physical and ecological conditions. The resources and forces on these groups are in a constant state of flux (due to advection and diffusion). As a result, small variations in effective predation pressure and competition can lead to large deviations as they build upon potentially large short-term changes in resources, the outcomes of these interactions can then accumulate or compound. However, as with all groups, the exact form of these responses to differing ecological and physical conditions are due to a mixture of trophic and non-trophic, as well as direct and indirect interactions. Thus, the greatest deviations are often seen when the simplified models are linear chains and furthest in form from the web of the standard case.

The relationship between trophic complexity and performance

Our findings that a high degree of simplification, whether by aggregating or omitting groups, leads to poor model performance is consistent with earlier studies (Sugihara et al. 1984, Costanza and Sklar 1985, Pahl-Wostl 1997). Simplification of trophodynamic models is possible, but thresholds exist beyond which insufficient detail

Figure 5.14: Comparison of the temporal dynamics of the biomass of diatoms (PL) in one cell (covering an input point from a sewage treatment plant) of the full Bay Model 2 model and versions with omitted groups when nutrient loads have been increased by fivefold. For clarity, only a selection of the runs has been displayed, but all the runs produced biomasses of PL between the extremes presented here.



remains to effectively reproduce the dynamics of complex systems. This is particularly crucial when successional or other sequential details are important. For example, without explicit representation of the size classes of phytoplankton, accurate bloom dynamics (and thus primary production) cannot be reproduced satisfactorily (Murray and Parslow 1997).

Unfortunately, the relationship between trophic complexity and performance is not linear, and is usually not even asymptotic. The overall measure *V*, as well as the relative spatial distributions and other indices, frequently suggest a more parabolic form to the pattern of performance over the entire range of simplification. This concurs with the findings of others (e.g Costanza and Sklar (1985)) for overall model performance with increasing complexity, as well as other studies of the effects of aggregating groups

(e.g. Gardner et al. 1982). The other relationship observed between trophic complexity and performance of the models is a threshold-triggered step-function. In the simplified models with aggregated groups, there is often a clear and sudden transition from a poor to a good performance when considering the relative spatial distributions of the components and processes (Table 5.8). This suggests that in these cases there is some minimum set required or some specific linkages that must be explicit for model behaviour to approach that of the full model. The most important of these triggers or critical requirements is the inclusion of both seagrass and macroalgae and the addition of benthic deposit feeders. This is not surprising given the overwhelming importance of these groups in large shallow marine systems (Harris et al. 1996) like the one modelled here.

Some mechanisms responsible for the shape of the response surfaces relating complexity and performance reported in previous studies (Gardner et al. 1982, Sugihara et al. 1984, Costanza and Sklar 1985, Rastetter et al. 1992) do not apply in our study. For example, in previous studies decline in performance with an increase in the number of components in the models was thought to be due to increasing effects of measurement error as more and more parameters were included. The models used here are all built with "perfect knowledge" of the standard system. Apart from the adjustments made to account for mortality due to groups no longer explicitly included in the simplified models, there is no adjustment of model parameters. It could be argued that model recalibration would be necessary even for models that omit groups, as the retuning represents "compensation" for the removal of explicit non-trophic interactions. However, these interactions can be exceedingly difficult to quantify even in a model setting. Moreover, an investigation of the effects of trophic simplification on model performance is more transparent without retuning. As there is no retuning and no measurement error to influence the behaviour of the simplified runs, the relative

performances can only be explained in terms of the adequate representation of the true web.

Empirical representation of subwebs

The explicit inclusion of a number, or even a majority, of the members and interactions of a particular subweb may not guarantee satisfactory model performance. If the subweb under consideration is strongly linked with another web, or if it is dependent on inputs from another web, then that other web must also be represented sensibly. For example, in large (1930 km^2) and shallow (≤24 m) systems such as the one modelled here, the inclusion of pelagos is a necessary requirement for an accurate representation of the benthos. The links between the pelagic and benthic communities in these systems are strong and consist of a number of trophic (predator-prey) and non-trophic (competitive) interactions. Consequently, simple forcing functions will not suffice, as evidenced by the poor performance of the OB and LB runs here. However, robust empirical representations of the pelagic-benthic link may be satisfactory. A good deal of attention has been paid to representing benthic returns to pelagic models (Fransz et al. 1991, Silvert 1991, McCreary et al. 1996), but empirical and explicit representation of the reverse needs more thought. The relative performance of the BM2 runs with and without explicit handling of the bacteria is evidence of how well an empirical sub-model can compensate for not explicitly representing a poorly, or incompletely, known component that has a potentially crucial role in the system. There is little if any improvement in overall model performance with the addition of bacteria to the simplified runs. In this case, given the effects of the other trophic simplifications on the model structure, the explicit inclusion of bacteria does not seem warranted. This is in contrast with the impressive increase in performance of the standard models after the addition of bacteria and an interactive form of the denitrification submodel (chapter

2).

Aggregation vs omission of groups

While the same broad effects of simplification are evident whether aggregating or omitting groups, omitting groups frequently has much less impact on performance than does aggregating groups. Previous consideration of the standard models has shown they reasonably reflect the biomass and dynamics of real systems (chapters 1 – 3). The standard models use food webs resolved to the level of functional groups (groups which share predators and prey, have similar degrees of mobility and metabolic rate constants within two to threefold of one another). The performance of the standard models implies that aggregation up to the level of functional groups is a valid method of handling complex systems. However, our results that aggregation of functional groups leads to poor model performance compared with omitting functional groups, indicates the presence of non-linear responses to aggregation of trophic complexity. It also indicates a "natural" level of aggregation. Thus, when simplifying a food web already aggregated to the level of functional groups, judicious choice and retention of the most important functional groups in a system appears to be a much more reliable method of constructing simplified webs than aggregating across functional groups in an effort to represent everything. One reason for this may be that aggregating functional groups breaks the "aggregation rules" laid down in previous studies. The web-like structure of natural systems means that aggregating functional groups produces an increasing number of instances where "serially-linked" aggregation cannot be avoided. This form of aggregation is known to be ill advised even at low levels of aggregation (Gardner et al. 1982). Further, aggregating functional groups often entails aggregating groups with rate constants more than two to threefold different to each other, which also appears to be ill advised (Wiegert 1977, O'Neill and Rust 1979, Cale and Odell 1980, Gardner et

al. 1982).

Changing ecosystem conditions and the stability-diversity debate

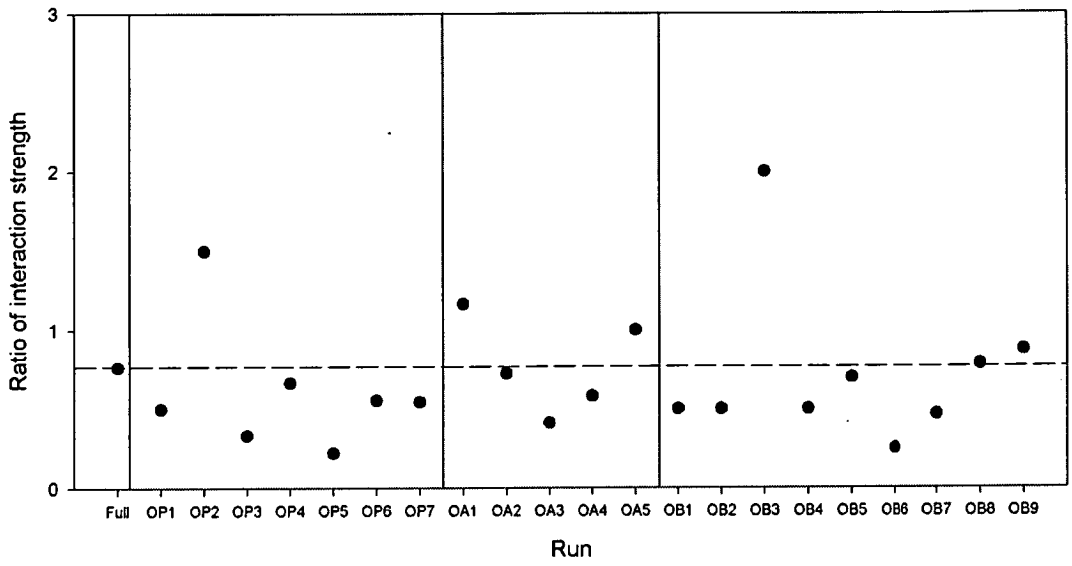
There are limitations to the approach of simplifying food webs by aggregating species to the level of functional groups and then omitting the least important functional groups. Predictions about system behaviour are often most wanted when there are large scale changes in external forcing, but this is when models that are too simplified fail to continue to faithfully reproduce system behaviour. Further, groups that may not have been important when the system was in one state may have a much greater role when conditions change. This is one of the fundamental ideas behind the ecological insurance hypothesis (Yachi and Loreau 1999). Formal consideration of which model with omitted groups performed the best under altered conditions is not possible, but it is nonetheless clear that the dynamics of models that are the least simplified are closest to the dynamics of the full models under changed nutrient loads. While the results are not as clear-cut in the scenario where fishing pressure is increased, the majority of the indices are closer to the standard for those runs with a minimum of simplification. This lends strong support to the suggestion that diversity provides natural communities with a buffer against change (Naeem and Li 1997, Naeem 1998, Yachi and Loureau 1999). Removing a few species will usually make little difference provided that the functional groups remain, as evidenced by the reliable performance of the standard runs, which only represent functional groups. Any further simplification of the system will have some effect, but it may be minimal if non-critical groups and interactions are lost. However, the full force of the effects of a loss in diversity will not present themselves until conditions have changed, as may arise given anthropogenic impacts on the environment. Thus, the behaviours of our simplified models are in agreement with the ecological insurance hypothesis.

The consideration of the effects of simplification by omission provides insight into another facet of the diversity-stability debate. It has been posited that connectance is a key factor in determining stability, but whether it improves (MacArthur 1955) or reduces (Gardner and Ashby 1970) stability is a matter of debate. There are no clear patterns of stability or performance in relation to connectance in the simplified models. This suggests that in webs that more closely resemble those in nature, it is not connectance *per se* but the identity of the links included that is important. Furthermore, the standard runs (that is the most complex runs) are stable, while other runs with fewer groups (but not the fewest) undergo self-simplification. Thus, the absolute number of components included in a model doesn't determine stability either, as was suggested in the early phases of the stability-diversity debate (Elton 1958, May 1973). One possible mechanism determining the system characteristics is the ratio of strong:weak interactions. Those runs with higher ratios of interaction strength (Figure 5.15) often exhibit instabilities, or trophic self-simplification or substantial departures in predicted distributions or total biomass for one or more groups. Moreover, the runs with the best overall performance are usually among those that had lower ratios of interaction strength (Figure 5.15). However, by itself the ratio of interaction strength is not a complete explanation as there are runs with low ratios that do not perform as well (e.g. OP3) and runs with high ratios that work reasonably well (e.g OB3). Simple rules of thumb do not completely describe behaviour of the models, at least not in this case. The details of the links and components included are also important.

5.5 Conclusions

By definition, ecosystem models are simplified versions of the real world systems they are designed to represent. The use of trophospecies or functional guilds has been a successful method for capturing system dynamics without requiring species runs simplified by omitting groups. The strength of each interaction was assessed using

Figure 5.15: Plot of the ratio of interaction strength (strong:weak) for the Bay Model 2 the availability parameters of the grazing term; availabilities greater than 0.5 were classed as strong interactions.



level detail (Fransz et al. 1991, Baretta et al. 1995, Murray and Parslow 1997, Baretta et al. 1998, chapters 1 – 3). However, even at this level models can be highly complex structures and for reasons of logistics, computational demands and intelligibility, further simplification can be attractive. The results of the simplifications performed here suggest that there are no simple answers to questions about trophic complexity and model performance. There is a clear indication that once the system has been aggregated to the level of the functional group further aggregation is unwise and complete omission of less important groups is a better option. Unfortunately, during model validation multiple models with varying levels of simplification will still be required to check whether critical components and links have been omitted. Even then the relative performance of the final simplified model may be inaccurate if the system is subject to large shifts in nutrient loads or exploitation levels. Our results suggest two general guides:

1) Reducing the complexity of a model web (which represents the food web of an

entire system aggregated to the level of functional groups) to less than 20 – 25% of its original size (whether through omission or aggregation of groups) is rarely beneficial. Overly simplified models lose too many of the feedbacks, and the trophic and non-trophic interactions that characterise the system and structure its behaviour. Representing the distinctions between the large and small flora and fauna, or mobile and sedentary fauna, may be crucial for success.

2) If an important process (e.g. denitrification) or linkage (e.g. pelagic-benthic coupling) is to be omitted from the model, then an empirical representation must be included if model performance is to be satisfactory.

These guides are in addition to any that have been stated elsewhere that deal with the added problems of measurement error and imperfect knowledge (Wiegert 1977, O'Neill and Rust 1979, Cale and Odell 1980, Innis and Rextad 1983, Halfon 1983 a and b, Gardner et al. 1982, Iwasa et al. 1987).

That it is not possible to find simple rules relating diversity with stability and other aspects of system behaviour in this study suggests that there may be no general solution to the stability-diversity debate. The results lend further credence to the ecological insurance hypothesis, but they do not suggest any simple relationship between connectance, or the ratio of interaction strength, and system behaviour and stability. Rather they imply that the biological details of the web, trophic as well as non-trophic, can be very important.

Chapter 6 Mortality and predation in ecosystem models: is it important how it is done?

Abstract

The effects of the form of the grazing and mortality terms used in plankton models are well known. The same cannot be said for ecosystem models. As ecosystem models become an increasingly utilised scientific tool more must be known about the effects of model formulation on model behaviour and performance. The impact of the form of the functional response and mortality terms used in a biogeochemical ecosystem model are considered here. We show that in the large and inter-linked webs used in ecosystem models, model behaviour is far more sensitive to the form of the grazing term than to that of the mortality terms used to close the modelled food web. In comparison with the simpler Holling disk equation, the most dynamic and sophisticated functional responses describing grazing require extra parameters and validation, but usually still lead to the same general conclusions about system state and the effects of changes in forcing functions. Thus, the use of more complex functional responses is not necessarily warranted in many cases. Similarly, the extra effort and data required to explicitly represent the top predators (sharks, mammals and birds) is not generally necessary, as a quadratic mortality term applied to intermediate predators (such as piscivores) is sufficient to achieve sensible model behaviour. However, it should be noted that some degree of sophistication is required in the grazing and mortality terms. Use of simple linear functional responses and mortality terms is unsuitable for models used to consider a range of nutrient loading or harvesting scenarios.

Keywords functional response, mortality term, model closure, biogeochemical, ecosystem, model, IGBEM, BM2

6.1 Introduction

Modern marine resource management is increasingly focused upon multiple use and sustainable management of marine systems. An important aspect of such a management approach is the use of appropriate tools. This is one of the driving forces behind the recent interest in ecosystem models (Walters et al. 1997, Hollowed et al. 2000, Sainsbury et al. 2000). These models, whether primarily biogeochemical or ecological, have a lot of potential, but several areas of their performance and structure need investigation.

While there are only a few accepted ways of handling the mechanics of hydrodynamics, biological processes can be formulated in a multitude of ways (Gao et al. 2000). In eutrophication models the issue of the effect of the formulation of biological processes on model performance has begun to be thoroughly analysed (Fransz et al. 1991, Edwards and Brindley 1999, Murray and Parslow 1999b, Edwards and Yool 2000, Gao et al. 2000, Tett and Wilson 2000). However, this has not been the case for ecosystem models that encompass whole food webs.

Due to their aims and scope, ecosystem models can often be quite large, highly detailed and potentially unwieldy. A comprehensive sensitivity analysis of parameters used in these models is often a daunting, if not impossible, task. Thus, the effects of alternative formulations of key processes may seem even less likely to be tackled. However, the work of Steele and Henderson (1992, 1995), Murray and Parslow (1999b) and Gao et al. (2000), amongst others, indicates that the behaviour of eutrophication models can be strongly dependent on these formulations. With the additional groups and linkages found in ecosystem models, it is unlikely that the effect of formulation is any less important.

Over the last quarter of a century theoretical and model studies have shown that the form of predation incorporated into models can have a large effect on their

performance (including stability) and predictions (May 1976, Hassel 1978, Hassell and Comins 1978, Begon and Mortimer 1986, Steele and Henderson 1992, Edwards and Brindley 1999, Gao et al. 2000). There are two areas in which predation and its formulation must be considered in biogeochemical models with multiple biological components. The first is the grazing terms used, which functional responses are implemented and whether these responses reasonably represent animal behaviour. The second is the formulation of the mortality terms for the species or groups at the highest trophic level of the web explicitly represented in the model. Natural mortality is applied to all biological components of models, but at the highest trophic levels in a model extra assumptions may be necessary. One important consideration is whether the effect of predators not explicitly covered in the web is constant or reacts to the size of the prey population, as one would expect populations of predators to respond. As a result, linear and quadratic mortality terms are the most common means of handling model closure (i.e. the mortality terms used for the top predators represented in the model). However, it is important to assess whether the model's behaviour is sensitive to the form of the mortality term used (Steele and Henderson 1992, Edwards and Brindley 1999, Murray and Parslow 1999b).

Examination of water quality models has indicated that the form of the grazing term used is not as important a determinant of model behaviour as the form of model closure employed (Steele and Henderson 1992, Edwards and Brindley 1999, Murray and Parslow 1999b, Edwards and Yool 2000). These investigations of the performance of water quality models also indicate that quadratic mortality is the most appropriate form of closing the food web in a model. Studies of the performance of water quality models also indicates that quadratic mortality appears to be the most appropriate form of closing the food web. Such studies have been restricted to planktonic webs and as there is little (if any) consideration of this topic in other areas of ecological modelling so

extension of these findings to larger webs is open to doubt.

Linear mortality is used in the majority of published ecological models without mention of its potential effects. In contrast, the effect of functional responses has received more widespread attention. Holling (1959) classified the range of relationships between consumption rate and prey density observed in nature into three "types": type I (linear increase in consumption rate with prey density up to some threshold density where consumption rate becomes constant); type II (smooth increase to an asymptote); and type III (sigmoidal). These three types are still widely used (Büssenschütt and Pahl-Wostl 2000), though they have been criticised for their simplicity and dependence on prey abundance. Much of the criticism has resulted from (1) the "boom and bust" predictions of models which use type I or II responses (Büssenschütt and Pahl-Wostl 2000); (2) the problem of the paradox of enrichment (where models predict only top predators will benefit from increased primary production, while empirical observations suggest all trophic levels benefit) (Hairstone et al. 1960, Arditi and Ginzburg 1989, Ginzburg and Akçakaya 1992); and (3) unrealistic behaviour at high predator abundance (Abrams 1993). As a result, other more complicated responses have been proposed. A review of all of these responses is beyond the scope of this paper, but it can be said that there have been mixed results and that the debate is far from over. For example, ratio-dependent responses were initially promising (Arditi and Ginzburg 1989, Matson and Berryman 1992), but their usefulness in general models (like the one considered here) has been questioned (Gleeson 1994, Sarnelle 1994, Abrams 1994, Abrams and Ginzburg 2000, Büssenschütt and Pahl-Wostl 2000). Nonetheless, functional responses, such as the one included in ECOSIM (Walters et al. 2000), which attempt to incorporate the pressure on an organism to maximise foraging time while minimising predation risk, are useful.

During the development of two biogeochemical ecosystem models, Bay Model 2

(BM2) (chapter 2) and the Integrated Generic Bay Ecosystem Model (IGBEM) (chapter 1), it became clear that the way in which feeding and mortality is modelled can be critical to model behaviour. For example, using only linear mortality terms for the fish groups in IGBEM (linear model closure) can result in unstable behaviour under some conditions (chapter 1). The work here examines some aspects of the effect of the form of the grazing terms and model closure on the dynamics and performance of an ecosystem model. This work is one part of a wider model study considering the effects of model structure and formulation on model behaviour.

6.2 Methods

To consider the effects of the formulation of the grazing term and model closure on model dynamics and performance, alternative forms of these terms are considered in the ecosystem model BM2. BM2 is a biogeochemical ecosystem model constructed at the level of trophic guilds. It follows the nitrogen and silicon pools of 21 living groups (pelagic and benthic) and a number of detrital and nutrient pools (Table 6.1). The food web (Figure 6.1) and associated processes are for a generic temperate bay system, rather than any particular bay. For convenience the physics used is a transport model built for Port Phillip Bay, in southern Australia, but the model captures the dynamics typical of many temperate coastal systems (chapter 2). An 8-box form of this model is used to investigate the alternative formulations considered. This spatial resolution provides a balance between computational requirements and potential impacts of model trophic self-simplification due to system homogeneity and refuge losses (chapter 4). There are some effects of self-simplification in the 8-box compared with the complete 59-box spatial configuration usually used with BM2 (Figure 6.2), but they are small and so the benefits of much shorter run times outweighs potential costs.

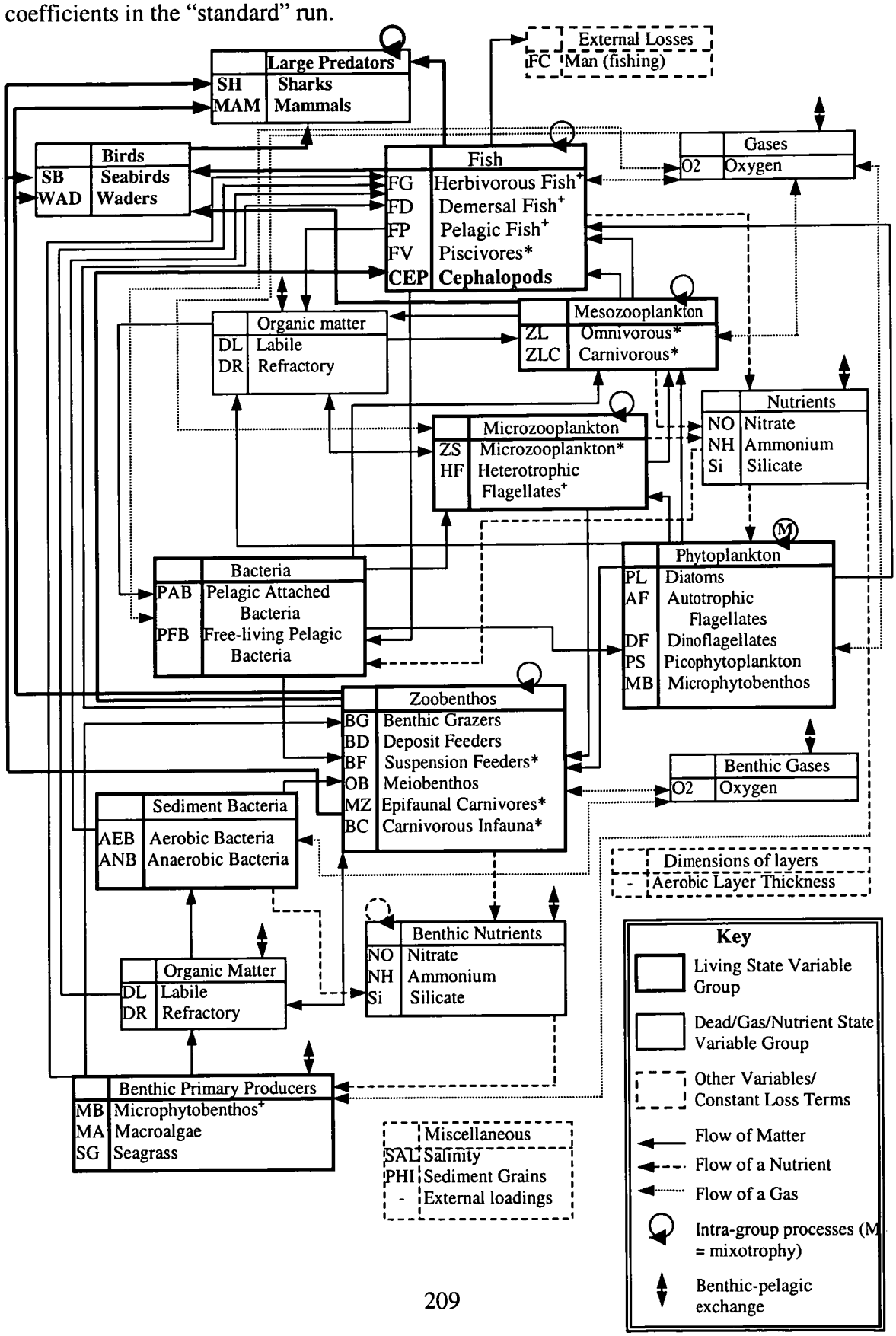
Table 6.1: Biologically associated components present in Bay Model 2 (BM2).

Component	Codename
Diatoms*	PL
Autotrophic flagellates	AF
Picophytoplankton	PS
Dinoflagellates	DF
Free-living pelagic bacteria	PFB
Pelagic attached bacteria	PAB
Heterotrophic flagellates	HF
Microzooplankton	ZS
Large omnivorous zooplankton	ZL
Large carnivorous zooplankton	ZLC
Planktivorous fish	FP
Piscivorous fish	FV
Demersal fish	FD
Demersal herbivorous fish	FG
Macroalgae	MA
Seagrass	SG
Microphytobenthos*	MB
Macrozoobenthos (epifaunal carnivores)	MZ
Benthic (epifaunal) grazers	BG
Benthic suspension feeders	BF
Infaunal carnivores	BC
Benthic deposit feeders	BD
Meiobenthos	OB
Aerobic bacteria	AEB
Anaerobic bacteria	ANB
Cephalopods^{+}	CEP
Seabirds^{+}	SB
Wading birds^{+}	WAD
Sharks^{+}	SH
Marine mammals^{+}	MAM
Labile detritus	DL
Refractory detritus*	DR
DON	DON
Ammonia	NH
Nitrate	NO
Dissolved silicate	Si
Dissolved oxygen	O2

* Also have an Si internal pool.

$^{+}$ Not present explicitly in the standard model, but added under one of the alternative model closure schemes.

Figure 6.1: Biological and physical interactions between the components used in Bay Model 2 (BM2). The flows (arrows) in bold are the linkages associated with the top predators (names in bold) that are not normally included explicitly in the web. Groups marked with * have both quadratic and linear mortality terms, as do those groups marked with a $^{+}$. However, the later have very small (<0.000001) quadratic mortality coefficients in the "standard" run.



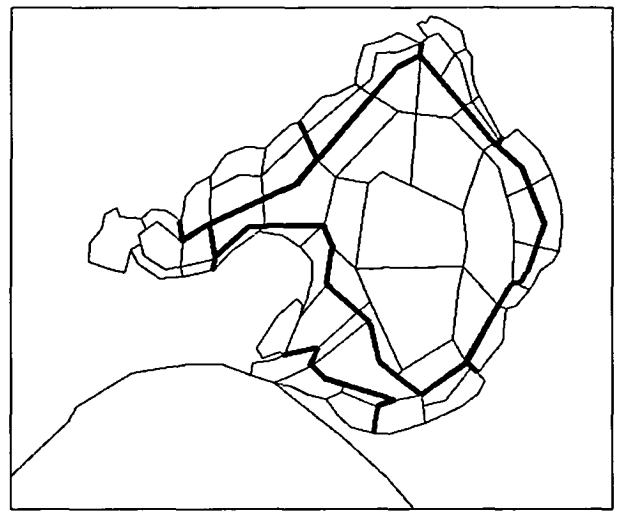


Figure 6.2: Spatial structure implemented for Bay Model 2 (BM2). The 8-box configuration marked in bold is the standard structure used for the runs discussed in this paper, while the 59-box structure is the default for BM2.

6.2.A Grazing functions

Six alternative grazing functions are trialled (Table 6.2). The formulations used are taken from the general ecological literature (Holling 1966, Begon and Mortimer 1986) or represent grazing formulations used in other ecological and ecosystem models (Baretta et al. 1995, Bryant et al. 1995, Ebenhöh et al. 1995, Walters et al. 2000). The formulations chosen cover a wide range of structural assumptions, from simple proportionality in the "type I" grazing term to complex behaviours trading predation risk against food requirements in the "ecosim-based" formulation. In each case the same grazing term is used for all consumers. This assumption that a single functional response is appropriate for all consumers, vertebrate and invertebrate alike, may not be valid. However, as there are no earlier studies to work from and as the modelled web is large and complex, it is considered to be an acceptable first step. Future studies may benefit from considering the effects of differing functional responses across the trophic levels.

6.2.B Mortality schemes

Four mortality (trophic closure) schemes are trialled. Unlike the grazing terms, the various schemes for trophic closure do not all represent completely different formulations. Every group in BM2 has a linear (or "basal") mortality term and any "special" mortality terms (due to bottom stress, eutrophication or oxygen stress) are applied separately to this "basal" mortality. In addition to these "basal" and "special" mortality terms the groups in each subweb which are predated upon by functional groups not explicitly included in the modelled web also have a quadratic mortality term. These groups (marked in Figure 6.1) are: heterotrophic flagellates, microzooplankton, large omnivorous zooplankton, large carnivorous zooplankton, microphytobenthos, planktivorous fish, piscivorous fish, demersal fish, demersal herbivorous fish, macrozoobenthos (epifaunal carnivores), benthic suspension feeders, and infaunal carnivores. The difference between the "standard", "no-linear" and "no-quadratic" mortality schemes is in the value given to the coefficients for linear and quadratic mortality applied to these groups. In the "standard" scheme both linear and quadratic mortality have non-zero coefficients. In the "no-linear" scheme the coefficient for the linear mortality term is set to zero and in the "no-quadratic" scheme the coefficient for the quadratic mortality term is set to zero. The final form of model closure considered ("top") involves extending the web to explicitly include more of the higher functional groups omitted (e.g. sharks) from the "standard" version of BM2 (these additional groups are in bold in Figure 6.1).

6.2.C Definition of the "standard" and alternative runs

For convenience each model run is given an identifying name (Table 6.3), which will be used for the remainder of this paper. The "standard" run is the run using the standard settings of BM2 – the top predators have non-zero linear and quadratic

Table 6.2: Alternative formulations of the grazing term ($G_{X,Y}$) per consumer considered. Additional crowding and oxygen limitation factors are not shown as they were only relevant in some groups.

Name	Equation	Definitions	Source
Standard (type II)	$G_{X,Y} = \frac{p_{X,Y} \cdot Y \cdot c_X}{1 + \frac{c_X}{l_X} \cdot \left(\sum_{ZZ} e_{X,Z} \cdot p_{X,Z} \cdot Z \right)}$	c_X = maximum clearance rate of predator X* $e_{X,Z}$ = assimilation efficiency of predator X on prey Z l_X = maximum growth rate of predator X* $p_{X,Y}$ = availability of prey YY to predator X Y = biomass of prey Y	Murray and Parslow 1997
Type I	$G_{X,Y} = \boldsymbol{min}\left(c_X \cdot p_{X,Y} \cdot Y, \frac{c_X}{l_X} \right)$	c_X = maximum clearance rate of predator X* l_X = maximum growth rate of predator X* $p_{X,Y}$ = availability of prey Y to predator X Y = biomass of prey Y	Murray and Parslow 1997
Type III	$G_{X,Y} = \frac{(p_{X,Y} \cdot Y)^2 \cdot c_X}{1 + \frac{c_X}{l_X} \cdot \left(\sum_{Z} e_{X,Z} \cdot (p_{X,Z} \cdot Z)^2 \right)}$	c_X = maximum clearance rate of predator X* $e_{X,Z}$ = assimilation efficiency of predator X on prey Z l_X = maximum growth rate of predator X* $p_{X,Y}$ = availability of prey Y to predator X Y = biomass of prey Y	Murray and Parslow 1997
Ecosim-like	$G_{XX,YY} = \frac{v_X \cdot T_X \cdot p_{X,Y} \cdot Y \cdot T_Y}{\frac{h_X \cdot T_X \cdot p_{X,Y} \cdot (1 + T_Y)}{1 + v_X \cdot \sum_Z Z \cdot T_Z} + v_X \cdot X \cdot T_X}$ where $T_X = \boldsymbol{min}\left(t_X, T_X^{prev} \cdot \left(1 - a_X + \frac{a_X \cdot Q_X}{\sum_Z G_{X,Z}^{prev}} \right) \right)$ and $Q_X = \sum_Z G_{X,Z}^{prev} \cdot \frac{\left(\frac{T_X^{prev}}{T_X^{older}} - 1 + a_X \right)}{a_X}$	a_X = feeding time adjustment factor (how quickly adjustments to relative feeding time occur) h_X = handling time of predator X G_X^{prev} = previous per consumer grazing for predator X $p_{X,Y}$ = availability of prey Y to predator X Q_X = optimal per consumer grazing for predator X v_X = search rate of predator X t_X = maximum relative feeding time allowed for predator X T_X = relative feeding time for predator X T_X^{prev} = previous relative feeding time for predator X T_X^{older} = relative feeding time for predator X from time period before last. T_Y = relative feeding time for predator Y T_Z = relative feeding time for predator Z X = biomass of predator X Y = biomass of prey Y	Christensen et al. 2000.

Table 6.2: Continued

Name	Equation	Definitions	Source
Bounded	$$G_{X,Y} = \frac{p_{X,Y} \cdot Y \cdot c_X \cdot l_X \cdot \left(\frac{{p_{X,Y}}^2 \cdot Y^2}{p_Y \cdot Y + k_X^l} \right)}{k_X^u + \sum_Z \frac{{p_{X,Z}}^2 \cdot Z^2}{p_{X,Z} \cdot Z + k_X^l}}$$	c_X = maximum clearance rate of predator X* k_X^l = lower prey biomass threshold for feeding by predator X k_X^u = half saturation coefficient for feeding by predator X l_X = maximum growth rate of predator X* $p_{X,Y}$ = availability of prey Y to predator X $p_{X,Z}$ = availability of prey Z to predator X Y = biomass of prey Y	Radford 1996
Dynamic search and handling	$$G_{X,Y} = \frac{p_{X,Y} \cdot Y \cdot V_X}{\left(1 + H_x \cdot V_X \cdot \sum_Z p_{X,Z} \cdot Z\right)}$$ where V_{XX} *and* H_{XX} are constants for non-finfish, but are size dependent for finfish such that $V_X = v_{a,X} \cdot {X_S}^{v_{b,X}}$ $H_X = h_{a,X} \cdot {X_S}^{-h_{b,X}}$	H_X = Handling time of predator X (as function of size in finfish, constant in other groups) $h_{a,X}$ = coefficient of handling time for finfish X $h_{b,X}$ = exponent of handling time for finfish X $p_{X,Y}$ = availability of prey Y to predator X $p_{X,Z}$ = availability of prey Z to predator X V_X = search rate of predator X (as function of size in finfish, constant in other groups) $v_{a,X}$ = coefficient of search rate for finfish X $v_{b,X}$ = exponent of search rate for finfish X X_S = structure weight of finfish X Y = biomass of prey Y	Radford 1996

* Temperature dependent. The standard Q_{10} temperature correction formula was used to adjust these rates, with a reference temperature of 15 degrees Celsius and a Q_{10} coefficient of 2.

mortality terms and all consumers use standard (type II) grazing terms. This run is used as the standard to compare against for the runs using alternative grazing terms and the runs using alternative trophic closure. Apart from this common run, consideration of the alternative (non-standard) grazing and mortality terms is done separately. For all the grazing term runs, the standard trophic closure (non-zero linear and quadratic mortality terms for the top predators) is used; and for all the model closure runs the standard grazing term (standard (type II)) is used. Consideration of the effects of different combinations of trophic closure and grazing terms, as well as different grazing terms for different functional groups (rather than one formulation applied to all groups), is left for future study.

6.2.D Parameter tuning

The original form of BM2 was calibrated by tuning the temperature-dependent maximum growth and mortality rates for all groups and the maximum clearance rates of the consumer groups (chapter 2). The final tuned values for these parameters are required to lie within the range of empirical estimates reported in the literature, rather than to match a specific set of observations (chapter 2). Consequently, limited re-tuning is allowed in each case investigated here. For the grazing terms, only those parameters in the grazing formulation are tuned, while for the mortality schemes only the mortality coefficients are modified for those groups present in the standard food web used in BM2. The additional groups added for the final mortality scheme are all calibrated in the same way as for the standard BM2 groups.

6.2.E Changing forcing conditions

The sensitivity of the model to different formulations is examined for "baseline" conditions. The examination is then repeated under various forcing conditions to gauge

Table 6.3: List of the identifying names given to the runs and sets of forcing conditions discussed in this paper.

Run name	Run details
Standard	Top predators have non-zero linear and quadratic mortality terms and all consumers use standard (type II) grazing terms
Grazing term runs	Mortality terms for top predators as of the standard run, only grazing terms differ between runs
bounded	Uses the equation for the Bounded functional response formulation in Table 6.2
dynamic	Uses the equation for the Dynamic search and handling functional response formulation in Table 6.2
ecosim-based	Uses the equation for the Ecosim-like functional response formulation in Table 6.2
type I	Uses the equation for the Type I functional response formulation in Table 6.2
type III	Uses the equation for the Type III functional response formulation in Table 6.2
Model closure runs	Grazing terms as of the standard run, only mortality terms for the top predators differ between runs
no-linear	Linear mortality term is set to zero for the top predators
no-quadratic	Quadratic mortality term is set to zero for the top predators
top	Marine mammals, seabirds, wading birds and cephalopods are explicitly included in the model

how the model's predictions regarding the effect of changing environmental conditions differ between runs using different formulations. The "baseline" conditions used the default nutrient forcing files and levels of fishing pressure for BM2 (chapter 2), while a change in environmental conditions is reflected by increasing the nutrient load or fishing pressure used by fivefold ("Nx5" and "Fx5" respectively). This degree of change in forcing conditions has previously been found to cause the standard form of BM2 to predict a change in system state, marked by substantial shifts in the biomass and spatial distribution of many of the modelled groups (chapter 2)

6.2.F Comparing the runs

Several measures are used to compare the various runs. These include the baywide average biomass per group, relative spatial distributions, the form of the temporal dynamics, and overall levels of pelagic, benthic and bacterial production and consumption. The degree of conformity between the relative spatial distributions predicted by the runs is evaluated using the number of boxes for which the relative spatial distribution of a functional group in a run using an alternative formulation differs from the distribution in the "standard" run. In contrast, the match between the temporal dynamics of the predicted time-series in the run using an alternative formulation and the "standard" run is ranked based on the matches between their respective shapes, amplitude, mean and timing. An exact match is given a rank of 1 and an additional 1 is added to this rank for each feature (shape, amplitude, mean or timing) which differs between the two time-series. Thus, a rank of 5 indicates no match in any feature between the time-series.

As the predicted value of the biomass, consumption and production per group may differ between runs under "baseline" conditions, simply repeating the comparison of these values for the runs under altered forcing conditions is not informative. Runs

predicting the same effects of changing forcing conditions may end up with different absolute results, because their "baseline" estimates differ and so the estimates under changing forcing conditions also differ. Thus, under altered conditions the relative change of a measure (average value under changed conditions / average value under "baseline" conditions) is a better choice, as it allows for the assessment of the predicted system changes in each run and it removes any potentially confounding effects caused by different runs predicting different values under "baseline" conditions.

The measures used here give a good indication of the effects of the various formulations on the model output and behaviour. However, since results for production and consumption reinforce the results based on biomass, and do not impart any new insights, they are not presented here.

6.3 Results

6.3.A Sensitivity to Grazing Terms

The relative differences between the average overall biomasses in the alternative runs indicates that under "baseline" conditions the "type I" grazing term produces results that are closest to those of the "standard" run (usually <30% difference). The run using a "bounded" grazing term shows the greatest overall divergence from the results of the "standard" run (with only 44% of the groups having predicted biomasses within 50% of the estimates from the "standard" run). This run is the only run where the majority of groups in the run is not within 50% of that predicted in the "standard" run (Table 6.4). However, even in the runs where the majority of groups are within 50%, there are a few groups (in particular those with high turnover rates) where the difference can be much larger (peaking at 507.95 times larger for meiobenthos in the "type III" run).

Considering the conformity of relative spatial distributions, it is clear that the

spatial distribution of some groups is influenced by the choice of grazing term and as a result there are some differences in spatial distributions between runs. The distributions for the "type I" run matches those of the "standard" run for all but the zooplankton groups, where there are some minor differences (Table 6.5). The other runs show more differences in their spatial distributions, primarily within those groups with faster dynamics (Table 6.5). The run employing the "bounded" grazing term shows the greatest degree of spatial divergence from the "standard" run. The "bounded" grazing term tends to predict evenly distributed populations where other grazing terms suggest stronger spatial structuring with local peaks in density (e.g heterotrophic flagellates, Figure 6.3).

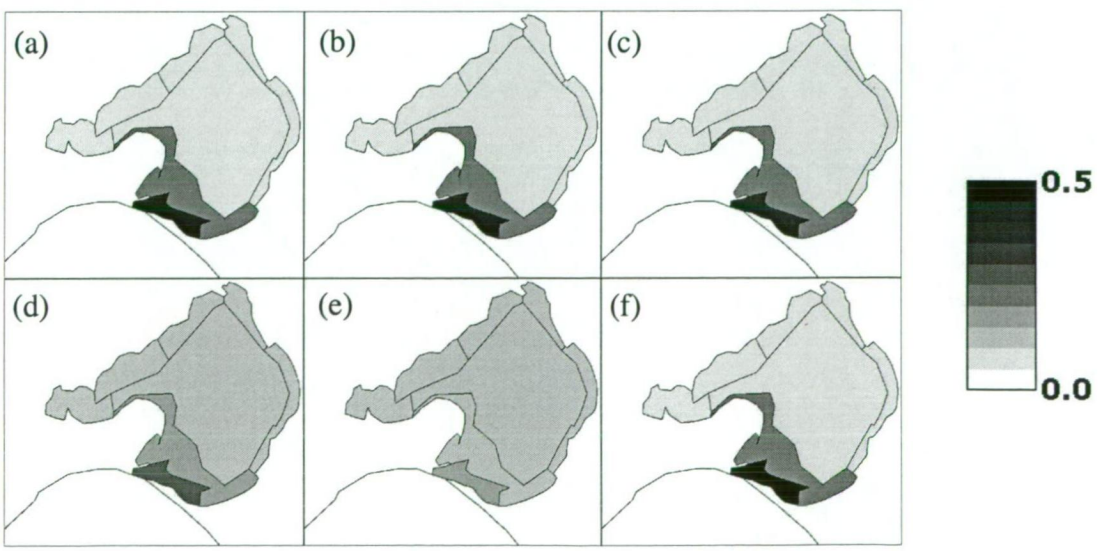
Table 6.4: Proportional difference between the biomass predicted in the "standard" run and those runs using alternative grazing formulations. Codes for the components are as of Table 6.1 and codes for the runs are as of Table 6.3.

Component	Type I	Type III	Ecosim-like	Bounded	Dynamic
AEB	0.06	0.46	1.64	2.09	0.88
AF	0.11	0.08	0.01	0.38	0.07
ANB	0.06	0.46	101.88	93.96	53.43
BC	< 0.01	1.04	0.60	0.08	0.07
BD	0.26	0.45	0.99	0.90	0.37
BF	0.03	0.09	0.25	0.86	0.15
BG	< 0.01	< 0.01	0.25	0.38	0.50
DF	0.05	0.49	0.50	0.50	0.05
FD	< 0.01	< 0.01	0.56	0.07	< 0.01
FG	0.04	0.03	0.71	0.47	0.32
FP	0.06	0.09	0.23	0.21	0.03
FV	0.16	0.80	0.06	0.21	0.08
HF	0.08	0.04	0.64	1.09	0.19
MA	0.19	0.21	0.08	1.00	1.00
MB	0.16	3.12	0.43	0.89	1.84
MZ	< 0.01	< 0.01	0.50	4.03	0.39
OB	0.91	507.95	220.73	261.18	22.98
PAB	0.04	0.16	0.71	1.09	0.81
PFB	0.01	0.27	2.95	5.60	3.42
PL	0.06	0.25	0.17	0.12	0.09
PS	0.08	1.37	9.57	4.94	9.14
SG	0.07	0.33	0.78	2.64	0.33
ZL	0.12	0.30	0.28	0.53	0.31
ZLC	0.28	1.76	0.38	0.07	0.02
ZS	0.19	0.13	0.32	0.17	0.19
Average	0.12	20.80	13.81	15.34	3.87

Table 6.5: Number of boxes for which the relative spatial distributions of the "standard" run differs from that predicted by the runs using an alternative grazing term. Codes for the components are as of Table 6.1 and codes for the runs are as of Table 6.3.

Component	Type I	Type III	Ecosim-like	Bounded	Dynamic
AEB	0	2	3	3	4
AF	0	0	1	7	1
ANB	0	5	2	2	5
BC	0	1	0	0	1
BD	0	0	0	0	0
BF	0	1	4	1	0
BG	0	0	1	3	0
DF	0	7	6	6	0
FD	0	0	0	0	0
FG	0	0	0	0	0
FP	0	0	0	0	0
FV	0	0	0	0	0
HF	0	0	2	7	0
MA	0	0	1	2	2
MB	0	1	1	3	4
MZ	0	0	4	5	2
OB	0	1	0	0	3
PAB	0	0	0	0	0
PFB	0	0	2	2	2
PL	0	1	5	5	5
PS	0	1	2	2	2
SG	0	1	0	1	1
ZL	1	1	1	1	1
ZLC	1	0	6	1	1
ZS	1	0	1	0	0

Figure 6.3: Proportion of the total average biomass of heterotrophic flagellates in each box for each run with alternative grazing formulations: (a) standard (type II), (b) type I, (c) type III, (d) ecosim-like, (e) bounded, and (f) dynamic.



The form of the time series for each group is generally more sensitive to the details of the grazing term than the time average values of the runs or the relative spatial distributions (Table 6.6). Runs with "type III" and "type I" functional responses are the least affected, with 30 – 40% of their component groups showing no difference to use of the "standard" grazing term. Runs using the other grazing functions diverge more from the "standard" model, though not all groups show major changes in their temporal dynamics (Table 6.6).

With changing nutrient loads and fishing pressure, some of the groups in the runs using alternative grazing terms have predicted biomass trends that diverge from the predicted trends in the "standard" run under the same change in forcing conditions (Tables 6.7 and 6.8). When nutrients increase ("Nx5"), the run employing the "ecosim-like" grazing term shows the greatest divergence from the "standard" run under the same conditions. In contrast, the run using "type I" grazing terms is the most different to the "standard" run when fishing pressure increases. The majority of groups in most runs using alternative grazing terms did follow the same general trends as for the "standard" run under the same changing forcing conditions. However, with an increase in fishing pressure, the predicted trend for the benthic deposit feeders in each of the runs using alternative grazing terms is consistently more than 1880 times the size of the trend predicted by the "standard" run (Table 6.8). The differences in the trends in biomass in the various runs are not just in size, but for some groups the predicted direction of change is also different (marked by a * in Table 6.7 and 6.8). For example, with an increase in nutrient loading (Table 6.8), the predicted change in biomass for the picoplankton in the run employing "ecosim-like" grazing terms is not only 2.92 times the magnitude of the trend in the "standard" run with an increasing nutrient load, but it is in the opposite direction (an increase rather than a decline).

Table 6.6: Quality of the match between the predicted time-series for each component in the "standard" run and those runs using alternative grazing formulations. Codes for the components are as of Table 6.1 and codes for the runs are as of Table 6.3. The entries are ranks indicating the degree to which the time-series matched that of the standard run. An exact match of the predicted time-series in the run using an alternative grazing term and the "standard" run has a rank of 1, and an additional 1 is added to this rank for each feature (shape, amplitude, mean or timing) which differs between the two time-series. Thus, a rank of 5 indicates no match in any feature between the time-series.

Component	Type I	Type III	Ecosim-like	Bounded	Dynamic
AEB	1	3	3	3	3
AF	3	5	5	5	5
ANB	1	3	5	5	5
BC	1	1	3	5	5
BD	3	3	5	5	3
BF	3	3	5	5	5
BG	1	1	2	3	1
DF	1	3	3	3	3
FD	1	1	5	5	2
FG	1	1	1	3	1
FP	1	1	1	2	1
FV	1	1	1	1	1
HF	5	5	5	5	5
MA	3	3	5	5	5
MB	5	5	5	5	5
MZ	1	1	5	5	4
OB	3	1	5	5	5
PAB	3	3	3	3	3
PFB	3	3	5	5	5
PL	3	3	5	5	5
PS	3	5	5	5	5
SG	2	3	5	5	4
ZL	3	5	5	5	5
ZLC	3	3	5	5	5
ZS	3	5	5	5	5

Table 6.7: Proportional difference between the change in biomass (average biomass under changing conditions / average biomass under "baseline" conditions) predicted in the "standard" run and those runs using alternative grazing formulations when the nutrient load is increased fivefold. Note that the Codes for the components are as of Table 6.1 and codes for the runs are as of Table 6.3.

Component	Type I	Type III	Ecosim-like	Bounded	Dynamic
AEB	4.64*	0.26	4.82*	5.61*	0.32
AF	0.04	0.12	0.11	0.85	0.32*
ANB	4.64	0.25	1.87*	1.38	0.12
BC	0.60	0.41	0.42	0.40	0.50
BD	0.15	0.69	0.40	0.40	0.63
BF	0.39	0.08	1.52*	1.43*	1.23*
BG	< 0.01	0.74	0.85	0.70	0.55
DF	0.03	< 0.01	0.01	0.01	0.12
FD	< 0.01	1.00	24.47*	0.36	< 0.01
FG	0.02	1.00	0.79	0.25	0.03
FP	0.01	1.00	0.60	0.16	0.30
FV	0.05	1.00	18.80	0.06	0.05
HF	0.06	0.09	0.08	0.11	0.12
MA	0.25	0.19	0.87*	0.77	0.78
MB	10.52	0.92*	0.57	0.83*	0.86*
MZ	< 0.01	0.00	0.63	0.80	0.35*
OB	0.81	1.00	1.00	1.00	1.00
PAB	0.29	0.06	0.15	0.34	0.09
PFB	< 0.01	< 0.01	0.01	0.20	0.14
PL	0.04	0.09	0.07	1.34*	0.20
PS	0.01	0.14	2.92*	0.96*	3.27*
SG	0.57	0.91	0.38	2.05	0.43
ZL	0.11	0.15	0.31	0.04	0.87
ZLC	< 0.01	0.20	0.34*	0.18	0.16
ZS	0.05	0.10	0.92*	3.79*	3.85*
Average	0.93	0.42	2.52	0.96	0.65

* The direction of change (increase or decline) predicted by the alternative formulation contradicted that of the "standard" run under the same conditions - for instance, a decline in place of an increase.

Table 6.8: Proportional difference between the change in biomass (average biomass under changed conditions / average biomass under "baseline" conditions) predicted in the "standard" run and those runs using alternative grazing formulations when the fishing pressure is increased fivefold. Codes for the components are as of Table 6.1 and codes for the runs are as of Table 6.3.

Component	Type I	Type III	Ecosim-like	Bounded	Dynamic
AEB	3.41*	0.40	0.70	0.69	0.68
AF	0.03	0.10	0.14	< 0.01	0.12
ANB	3.44*	0.40	0.73	0.73	0.70
BC	0.52	0.16	0.52	0.52	0.52
BD	3739.49*	1887.85*	3312.18	3321.52	3543.97
BF	0.17*	0.21	0.08	0.07	0.08
BG	1.67	0.31	2.09*	1.64	1.67
DF	0.04	0.01	0.01	0.01	0.01
FD	0.05	< 0.01	2.05	0.11	3.08
FG	0.07	0.03	0.46	0.11	0.98
FP	0.01	0.08	1.60	0.30	1.78
FV	0.18	0.45	0.05	0.64	0.68
HF	0.05	0.13	0.21*	0.18	0.15
MA	0.06	0.30	0.07	0.10	0.10
MB	0.62*	0.51	0.15*	0.22*	0.08
MZ	0.15	0.15	0.22*	0.14	0.16
OB	1.00*	1.00	1.00	1.00	1.00
PAB	0.19	0.06	0.05	0.08	0.09
PFB	0.01	< 0.01	0.07*	0.01	0.01
PL	0.20	0.01	0.10	0.12	0.04
PS	0.11	0.44	0.57*	0.03	0.45
SG	0.32	0.25	0.31	0.31	0.31
ZL	0.28	0.31	0.03	0.44	0.25
ZLC	0.18	0.69	0.64	0.63	0.63
ZS	3.59*	0.34	1.73	1.72	1.85
Average	150.23	75.77	133.03	133.25	142.38

* The direction of change (increase or decline) predicted by the alternative formulation contradicted that of the "standard" run under the same conditions - for instance, a decline in place of an increase.

In the runs using the alternative grazing terms, there is an increase in the number of groups with spatial and/or temporal patterns which do not conform with those of the "standard" run under the same change in forcing conditions (Tables 6.9 and 6.10). The most noticeable differences are for groups in the "type I" run. Under "baseline" conditions, the relative distributions of all groups in the run with "type I" grazing terms conform with the relative distribution in the "standard" run for 7 or more boxes. In contrast, when nutrient loading increases fivefold ("Nx5"), only 68% of the groups in the run using "type I" grazing terms conform with the relative distribution predicted by the "standard" run, under the same conditions, for 7 or more boxes (Table 6.9). Similarly, with changing forcing conditions, there are an increasing number of groups in the run using "type I" grazing terms that have time-series that differ markedly from the form of the time-series in the "standard" run under the same forcing conditions (Table 6.10).

6.3.B Sensitivity to the form of mortality used in model closure

The relative difference between the baywide mean biomasses of the "standard" run and the runs using alternative forms of model closure indicates that under "baseline" conditions the greatest changes occur when the linear mortality term is set to zero for those groups which have predators not explicitly represented in the modelled web (Table 6.11). Generally, the run ("top") where the top predators (sharks, mammals and birds) are included explicitly shows the least divergence from the "standard" run, with predicted biomasses usually within 5% of the "standard" run. There is no run using an alternative form of model closure for which the predicted biomasses of the majority of the groups are not within 50% of the estimates in the "standard" run. However, there are still some groups in each run which differed substantially from the estimate in the "standard" run (the largest difference is for benthic deposit feeders in the run with the

"no-linear" model closure, which differ from the "standard" run by 355%).

Table 6.9: Number of boxes for which the relative spatial distributions of the "standard" run differs from that predicted by the runs using an alternative grazing term when forcing conditions are changing. Codes for the components are as of Table 6.1 and codes for the runs are as of Table 6.3. The columns headed Nx5 are the patterns when nutrient loading rises fivefold and those headed Fx5 were from the runs where the fishing pressure rises fivefold.

	Type I		Type III		Ecosim-like		Bounded		Dynamic	
Component	**Nx5**	**Fx5**	**Nx5**	**Fx5**	**Nx5**	**Fx5**	**Nx5**	**Fx5**	**Nx5**	**Fx5**
AEB	5	2	1	7	3	4	3	4	0	1
AF	2	6	6	6	3	5	1	1	6	2
ANB	5	3	1	6	3	4	3	4	1	0
BC	4	1	1	0	1	1	1	1	1	0
BD	0	0	1	0	1	0	1	0	1	1
BF	6	1	4	3	6	5	6	2	6	1
BG	0	0	0	0	1	1	2	2	2	0
DF	0	0	7	7	6	6	6	6	0	0
FD	0	0	0	0	0	0	0	0	0	0
FG	0	0	0	0	0	0	0	0	0	0
FP	0	0	0	0	0	0	0	0	0	0
FV	0	0	0	0	0	0	0	0	0	0
HF	0	0	0	0	6	0	7	7	1	1
MA	0	0	0	0	3	1	2	2	2	2
MB	4	0	2	0	1	2	1	3	1	4
MZ	0	0	0	0	4	4	6	5	1	2
OB	4	1	4	4	4	1	4	1	5	5
PAB	0	0	0	0	0	0	0	0	0	0
PFB	0	0	0	0	2	2	2	2	2	2
PL	5	1	2	1	4	4	2	0	5	1
PS	0	0	1	1	2	2	2	2	2	2
SG	1	1	2	0	2	1	2	2	3	0
ZL	0	0	1	1	0	0	1	0	0	1
ZLC	0	1	1	0	7	2	0	1	0	1
ZS	1	6	0	6	0	6	3	6	4	6

Table 6.10: Quality of the match between the predicted time-series under changing forcing conditions for each component in the "standard" run and those runs using alternative grazing formulations. Codes for the components are as of Table 6.1, codes for the runs are as of Table 6.3, meaning of the ranks as for Table 6.6. The columns headed Nx5 are the patterns when nutrient loading rises fivefold and those headed Fx5 were from the runs where the fishing pressure rises fivefold.

	Type I		Type III		Ecosim-like		Bounded		Dynamic	
Component	**Nx5**	**Fx5**	**Nx5**	**Fx5**	**Nx5**	**Fx5**	**Nx5**	**Fx5**	**Nx5**	**Fx5**
AEB	3	3	3	3	3	3	3	3	4	3
AF	5	3	5	5	5	5	5	5	5	5
ANB	3	3	3	3	5	5	5	5	5	5
BC	1	1	1	1	5	3	5	5	5	5
BD	2	3	1	3	5	5	5	5	2	3
BF	5	5	3	5	5	5	5	5	4	5
BG	1	1	1	1	5	5	3	2	5	1
DF	3	3	3	3	3	3	3	3	3	3
FD	1	1	1	1	5	5	3	1	2	5
FG	1	1	1	1	5	1	1	1	1	1
FP	1	4	1	1	5	5	2	4	2	4
FV	1	1	1	1	5	1	1	1	1	1
HF	5	5	5	3	5	3	5	3	5	3
MA	3	3	1	3	5	5	5	5	5	5
MB	4	3	5	5	5	3	5	5	5	5
MZ	1	1	1	1	3	3	5	5	4	3
OB	5	5	5	1	5	5	5	5	5	5
PAB	3	3	1	3	3	3	3	5	3	1
PFB	3	3	3	3	5	5	5	3	5	5
PL	3	3	5	3	5	5	5	5	5	5
PS	3	5	5	5	5	5	5	5	5	5
SG	5	3	3	3	5	5	5	4	5	3
ZL	3	5	5	5	5	5	5	5	5	5
ZLC	3	5	5	5	5	5	5	5	5	5
ZS	3	3	5	5	5	5	5	5	5	3

Table 6.11: Proportional difference between the biomass predicted in the "standard" run and those runs using alternative forms of model closure. Codes for the components are as of Table 6.1 and codes for the runs are as of Table 6.3.

Component	Top	No-linear	No-quadratic
AEB	0.01	0.97	1.00
AF	0.01	0.58	0.01
ANB	0.01	0.97	1.00
BC	< 0.01	2.41	0.66
BD	1.11	3.55	0.44
BF	< 0.01	0.77	0.34
BG	< 0.01	0.12	0.49
DF	< 0.01	0.29	0.16
FD	< 0.01	< 0.01	< 0.01
FG	< 0.01	0.26	0.03
FP	< 0.01	< 0.01	< 0.01
FV	0.04	0.01	0.01
HF	< 0.01	0.60	0.03
MA	0.17	0.96	0.22
MB	0.01	0.74	0.82
MZ	< 0.01	0.18	0.29
OB	1.00	1.00	1.00
PAB	0.02	0.55	0.50
PFB	< 0.01	0.02	< 0.01
PL	0.01	0.15	0.02
PS	0.02	0.34	0.15
SG	0.02	2.54	2.45
ZL	< 0.01	0.03	0.02
ZLC	0.01	0.02	0.03
ZS	0.03	0.19	0.11
Average	0.10	0.69	0.39

While there are some dissimilarities between the relative spatial distributions of the "standard" run and the runs using alternative forms of model closure, these differences are not as large as for some of the runs using alternative grazing functions. The relative spatial distributions of each group, in the run where the top predators are included explicitly ("top"), are identical to those of the "standard" run, except for the meiobenthos where the distribution matches that of the runs using the other alternative forms of model closure. The runs where there is "no-linear" or "no-quadratic" mortality do not show as much spatial conformity (with the "standard" run) as the "top" run. The

run using an alternative model closure scheme that has the poorest spatial conformity with the "standard" run is "no-linear". In this run only 40% of the groups have relative distributions which match the "standard" run and 24% of the groups have spatial distributions that suggest a more widespread population, or one that is centred in a different part of the bay, to that predicted by the "standard" model run (Table 6.12). The spatial conformity of the run with "no-quadratic" model closure is better, with the relative distributions of a majority of the groups matching the distributions predicted by the "standard" run. The "no-linear" and "no-quadratic" model closure runs do not conform as well with the "standard" run as the "top" run, but they are closer than some

Table 6.12: Number of boxes for which the relative spatial distribution of the "standard" run differs from that predicted by the runs using an alternative forms of model closure. Codes for the components are as of Table 6.1 and codes for the runs are as of Table 6.3.

Component	Top	No-linear	No-quadratic
AEB	0	2	2
AF	0	1	0
ANB	0	2	3
BC	0	1	1
BD	0	0	0
BF	0	5	7
BG	0	1	0
DF	0	4	1
FD	0	0	0
FG	0	0	0
FP	0	0	0
FV	0	0	0
HF	0	2	0
MA	0	0	0
MB	0	1	1
MZ	0	0	0
OB	2	2	2
PAB	0	1	1
PFB	0	0	0
PL	0	1	0
PS	0	1	0
SG	0	1	1
ZL	0	0	0
ZLC	0	0	1
ZS	0	1	0

of the runs using alternative grazing terms. In the runs using "ecosim-like", "bounded" or "dynamic" grazing terms 36 – 48% of the relative distributions differed by more than 2 boxes from the distribution predicted by the "standard" run (Table 6.5).

The form of the patterns observed in the time-series of each group is dependent on the form of model closure used. The run with explicit top predators included ("top") shows the least effect of using alternative model closures, while the other two configurations are more heavily impacted (Table 6.13). For each run there are some groups that show the same form of time-series as the "standard" run, and these are mostly the slower growers (fish and benthic groups). However, each of the runs using an alternative form of model closure also has groups whose time-series do not match that of the "standard" run (Table 6.13). In some cases (e.g. for the large carnivorous zooplankton) the differences are only minor, with the same general pattern holding regardless of the form of closure used, but where there are changes in the amplitude or the mean or timing of the pattern (Figure 6.4). In other cases (e.g. the meiobenthos) the change in temporal dynamics is striking (Figure 6.5).

When fishing pressure is increased, there is little difference in the overall performance of the runs using the alternative forms of model closure, though the run employing the "no-quadratic" model closure does diverge slightly more from the "standard" run than the others (Table 6.14). When nutrient loading is increased the run using "no-quadratic" model closure diverges from the "standard" run much more than does either of the other two alternatives (Table 6.15). When nutrient loads or fishing pressure are increased, the predicted trends for the sediment infauna (macro- or microscopic) can be orders of magnitude larger in runs using alternative model closure than for the "standard" run, under the same conditions (Tables 6.14 and 6.15). For example, when fishing pressure increases fivefold the change in biomass for the benthic deposit feeders is more than 3442 times that of the "standard" run in all the runs using

Table 6.13: Quality of the match between the predicted time-series for each component in the "standard" run and those runs using alternative forms of model closure. Codes for the components are as of Table 6.1, codes for the runs are as of Table 6.3, meaning of the ranks as for Table 6.6.

Component	Top-predators explicit	No-linear	No-quadratic
AEB	1	3	5
AF	3	5	3
ANB	1	3	5
BC	1	1	5
BD	3	3	5
BF	1	5	5
BG	1	1	1
DF	1	2	1
FD	5	1	1
FG	5	1	1
FP	5	1	1
FV	5	1	1
HF	1	3	2
MA	2	3	3
MB	1	3	3
MZ	1	1	3
OB	5	5	5
PAB	1	3	3
PFB	2	3	3
PL	2	3	2
PS	3	5	2
SG	1	3	3
ZL	2	4	2
ZLC	3	3	2
ZS	3	3	1

Figure 6.4: An example of only minor differences in time-series for alternative forms of model closure. Shown here is the biomass of large carnivorous zooplankton (ZLC) in box 8 (in the centre of the bay) over the same four-year period for runs using the "standard", "no-linear" and "no-quadratic" forms of model closure.

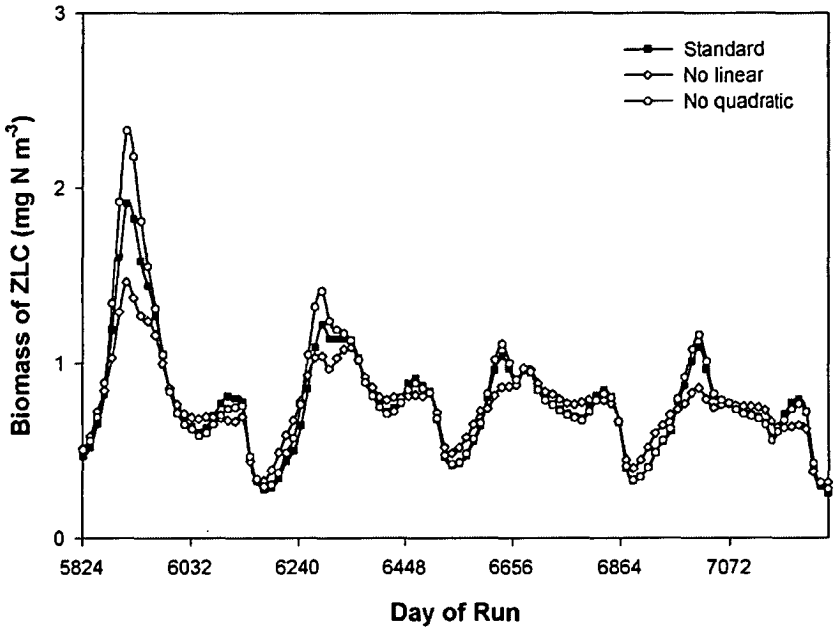


Figure 6.5: An example of major differences in time-series for alternative forms of model closure. Shown here is the biomass of autotrophic flagellates (AF) in box 8 (in the centre of the bay) over the same four-year period for the runs using the "standard" and "no-linear" forms of model closure.

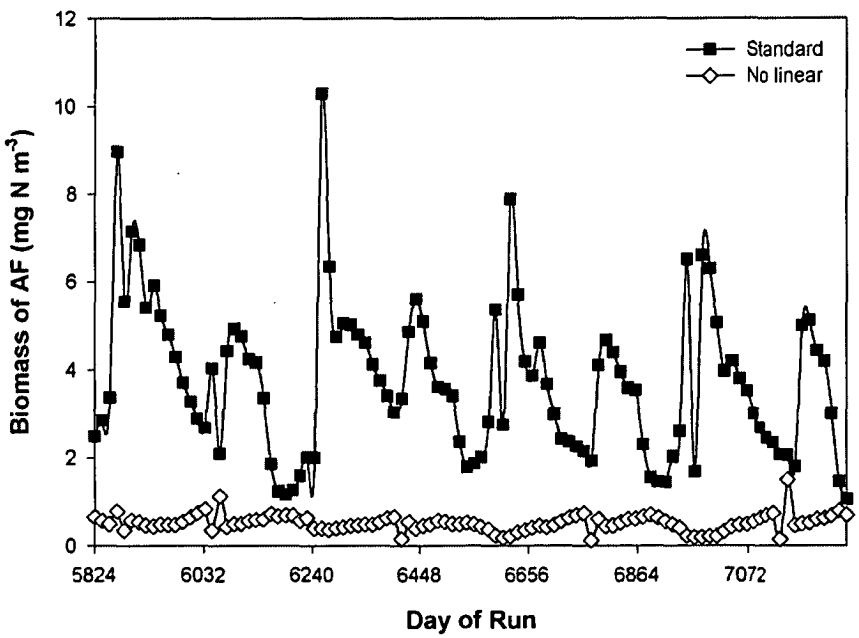


Table 6.14: Proportional difference between the change in biomass (average biomass under changed conditions / average biomass under "baseline" conditions) predicted in the "standard" run and those runs using alternative forms of model closure when the fishing pressure is increased fivefold. Codes for the components are as of Table 6.1 and codes for the runs as of Table 6.3.

Component	Top-predators explicit	No-linear	No-quadratic
AEB	0.81	0.87	0.38
AF	< 0.01	0.16	0.03
ANB	0.82	0.88	0.69
BC	0.52	0.52	0.52
BD	3442.71	3333.79	3587.31
BF	0.13	0.05	0.42
BG	1.67	1.69	1.67
DF	0.02	0.01	0.10
FD	0.02	0.01	< 0.01
FG	< 0.01	0.07	0.05
FP	0.02	< 0.01	< 0.01
FV	0.05	< 0.01	0.01
HF	0.02	0.02	0.01
MA	0.14	0.10	0.08
MB	0.06	0.04	0.03
MZ	0.15	0.15	0.15
OB	1.00	1.00	1.00
PAB	0.16	0.09	0.17
PFB	< 0.01	0.01	< 0.01
PL	0.05	0.04	0.07
PS	0.02	0.44	0.13
SG	0.29	0.31	0.31
ZL	0.02	< 0.01	0.06
ZLC	0.02	0.05	0.03
ZS	0.03	0.14	0.02
Average	137.95	133.62	143.73

Table 6.15: Proportional difference between the change in biomass (average biomass under changed conditions / average biomass under "baseline" conditions) predicted in the "standard" run and those runs using alternative forms of model closure when the nutrient load is increased fivefold. Codes for the components are as of Table 6.1 and codes for the runs as of Table 6.3.

Component	Top-predators explicit	No-linear	No-quadratic
AEB	< 0.01	0.93	38.02*
AF	0.02	0.16	0.05
ANB	< 0.01	0.98	9.13*
BC	< 0.01	0.77	0.80
BD	0.42	0.51	0.54
BF	< 0.01	0.24	1.49*
BG	< 0.01	0.10	< 0.01
DF	< 0.01	< 0.01	0.20
FD	< 0.01	< 0.01	< 0.01
FG	< 0.01	0.19	0.01
FP	< 0.01	0.02	0.01
FV	< 0.01	0.08	0.06
HF	0.01	0.11	0.06
MA	0.10	0.45	0.21
MB	< 0.01	0.67*	0.65
MZ	< 0.01	< 0.01	< 0.01
OB	31.23	1.00*	1.00
PAB	0.01	0.46	0.49
PFB	< 0.01	0.01	0.01
PL	0.01	0.08	0.02
PS	0.03	0.13	0.05
SG	0.07	0.76	0.01
ZL	0.01	0.20	0.13
ZLC	0.01	0.17	0.13
ZS	0.01	0.05	0.06
Average	1.28	0.32	2.13

* The direction of change (increase or decline) predicted by the alternative formulation contradicted that of the "standard" run under the same conditions - for instance, a decline in place of an increase.

alternative forms of model closure (Table 6.14). Once again there are a few cases where the differences in the trends go beyond differences in magnitude. However, the only groups for which the predicted trend in biomass is in the opposite direction to the trend in the "standard" run, under the same conditions, are in the runs employing "no-linear" and "no-quadratic" mortality when nutrient loading increases (Table 6.15).

Generally, for the runs using "no-linear" model closure or explicit top predators ("top"), spatial and temporal conformity with the patterns predicted by the "standard" run are as good under changing forcing as under "baseline" conditions (Tables 6.16 and 6.17). This is not the case for either of the runs using "no-quadratic" mortality when forcing conditions change. When nutrient loads or fishing pressure increases there is a reduction in the number of groups for which the patterns predicted by the run with "no-quadratic" mortality match those of the "standard" run (Tables 6.16 and 6.17). More generally, under changing forcing conditions, any differences in the spatial patterns observed in the runs employing alternative forms of model closure are usually stronger than under "baseline" conditions (Table 6.16). Such a consistent result is not evident for the form of the temporal dynamics predicted in each run (Table 6.17).

6.4 Discussion

Given their direct impact throughout the web, rather than just at higher trophic levels, it is not surprising that the effects of alternative grazing terms were larger and more pervasive than those due to using different forms of model closure. However, this does not agree with the findings of Steele and Henderson (1992) or Murray and Parslow (1999b). They found that the form of the model closure was generally far more important in determining model behaviour than internal details, such as the functional responses of consumers. This difference may reflect that the web used in the ecosystem model investigated here incorporates many more consumers in a more highly

Table 6.16: Number of boxes for which the relative spatial distributions of the "standard" run differs from that predicted by the runs using an alternative forms of model closure when forcing conditions are changing. Codes for the components are as of Table 6.1 and codes for the runs as of Table 6.3. The columns headed Nx5 are the patterns when nutrient loading rises fivefold and those headed Fx5 were from the runs where the fishing pressure rises fivefold.

	Top-predators explicit		No-linear		No-quadratic	
Component	**Nx5**	**Fx5**	**Nx5**	**Fx5**	**Nx5**	**Fx5**
AEB	0	4	4	4	3	4
AF	0	0	1	1	0	0
ANB	0	4	4	4	7	5
BC	0	1	8	2	8	2
BD	0	0	1	0	1	0
BF	0	1	2	3	4	5
BG	0	0	0	1	0	0
DF	0	0	4	5	1	1
FD	0	0	0	0	0	0
FG	0	0	0	0	0	0
FP	0	0	0	0	0	0
FV	0	0	0	0	0	0
HF	0	0	3	6	0	0
MA	0	0	0	0	0	0
MB	1	0	2	1	2	1
MZ	2	3	0	3	1	4
OB	0	3	4	3	4	3
PAB	0	0	1	1	0	1
PFB	0	0	0	0	0	0
PL	0	0	2	1	0	2
PS	0	0	1	0	0	0
SG	0	1	1	2	2	2
ZL	0	0	0	0	0	0
ZLC	0	0	1	0	0	0
ZS	0	0	1	1	0	1

Table 6.17: Quality of the match between the predicted time-series under changing forcing conditions for each component in the "standard" run and those runs using alternative forms of model closure. Codes for the components are as of Table 6.1, codes for the runs are as of Table 6.3, meaning of the ranks as for Table 6.6. The columns headed Nx5 are the patterns when nutrient loading rises fivefold and those headed Fx5 were from the runs where the fishing pressure rises fivefold.

	Top-predators explicit		No-linear		No-quadratic	
Component	Nx5	Fx5	Nx5	Fx5	Nx5	Fx5
AEB	1	3	5	3	5	5
AF	3	3	5	5	3	3
ANB	1	1	5	5	5	5
BC	1	1	1	1	5	5
BD	1	3	1	3	5	5
BF	1	3	5	5	5	5
BG	1	1	1	1	1	1
DF	1	1	3	1	3	3
FD	5	1	1	1	1	1
FG	5	4	1	1	1	1
FP	5	5	1	3	1	4
FV	5	1	1	1	1	1
HF	1	3	2	3	2	5
MA	1	1	1	3	3	3
MB	1	1	5	5	5	3
MZ	1	1	3	1	3	3
OB	3	5	5	5	5	5
PAB	1	3	3	3	3	3
PFB	1	3	3	5	3	3
PL	1	3	3	3	3	3
PS	3	1	3	3	3	5
SG	2	1	5	3	5	3
ZL	3	2	3	3	3	3
ZLC	3	1	3	1	3	3
ZS	2	3	3	3	3	3

interconnected web than the simple Nutrient-Phytoplankton-Zooplankton chains considered by Steele and Henderson (1992) and Murray and Parslow (1999b).

Functional responses

The sensitivity of model behaviour to the form of the grazing term, especially under changing ecosystem conditions, indicates that careful thought must be given to the choice of grazing term and the associated assumptions and data requirements. For

the simpler "Holling-type" functional responses, the behaviour of the model under "baseline" conditions indicates that the biomasses of the various prey groups are at a level where the potentially destabilizing nature of the simpler functional responses (Begon and Mortimer 1986) is of little importance. There are the occasional exceptions (like meiobenthos when using the "type III" response), but overall there is very little difference in the outcome of the standard, "type I" and "type III" runs under "baseline" conditions. This is because the prey biomasses keep the functional response curves within a section where they are similar to each other (Figure 6.6). This finding is similar to that of previous studies (Gao et al. 2000, Tett and Wilson 2000). It is only under increasing nutrient loads and/or fishing pressures that the differences in the curves influence model behaviour as the biomasses become very large or small (depending on the prey groups in question). Even under these more extreme conditions there is little to

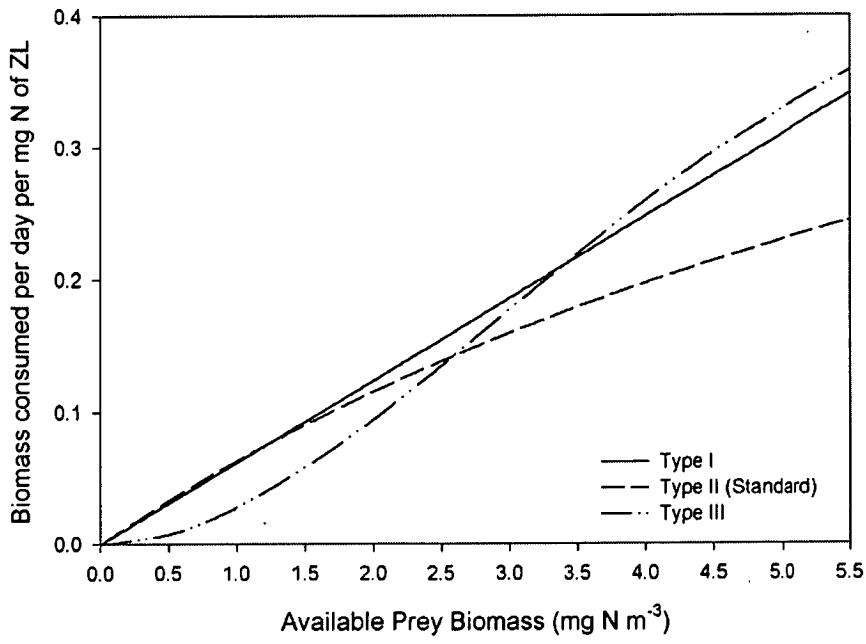


Figure 6.6: The "type 1", "type II" (the response used in the standard run) and "type III" functional responses for the large omnivorous zooplankton (ZL). The range of prey biomasses shown covers the typical levels of available prey biomass, although the available biomass can jump to much higher levels (2 – 5 fold higher) for short periods during bloom events.

recommend the general use of a Type III curve over that of a Type II if coefficients of prey availability feature in the formulations (as they do in this case). However, in the mixed case, where the same functional response is not applied to all groups, selective use of a Type III may prove to be beneficial for those groups whose behaviour in the field matches the formulation's assumptions.

The simple "Holling-type" functional responses are used widely in food chain and ecosystem models (Büssenschütt and Pahl-Wostl 2000), but they are not the only functional responses employed. Other functional responses in use include: the modified disk equation that incorporates thresholds (Radach and Moll 1993, Baretta et al. 1995, Tett and Wilson 2000); the Ivlev formula (McGillicuddy et al. 1995); ratio-dependent functions (Arditi and Ginzburg 1989, Matson and Berryman 1992); and a two-dimensional function of the biomasses of predator and prey (Büssenschütt and Pahl-Wostl 2000). Consideration of the complete list of functional responses is beyond the scope of our work and recent work suggests that ratio-dependent functions may not be suitable for use in general models such as BM2 (Gleeson 1994, Sarnelle 1994, Abrams 1994, Abrams and Ginzburg 2000, Büssenschütt and Pahl-Wostl 2000). Conversely, the arguments regarding the effects of thresholds (Frost 1975, Bryant et al. 1995) and the impacts on behaviour and feeding of groups other than the predator and prey (Abrams and Ginzburg 2000, Walters et al. 2000) are well made. For this reason we examined the effects of using "bounded", "dynamic" and "ecosim-like" functional responses. The effects of using these formulations are often greater than moving from the standard to "type I" or "type III" functional responses. They also tend to have greatest impact on groups that are poorly known or only beginning to attract attention in biogeochemical models (such as infauna, flagellates and bacteria). For many of these groups the behaviour under the more sophisticated functional response is no closer to real biomass dynamics than that achieved with the simpler standard functional response. However,

the performance of the benthic deposit feeding group is substantially improved, particularly when nutrient loading increases. The behaviour of this group is a weakness of the standard form of BM2 (chapter 2), which seems to be corrected if the additional checks inherent in the more complex functional responses are added. By itself however, this is no reason to include high levels of added complexity in functional responses across all groups as a matter of course. While the "type I" functional response is obviously insufficient if the model is to behave realistically as conditions change, careful thought must be given to how much flexibility should be added - to how many feedbacks, thresholds and inflexion points are added – when more sophisticated responses are used. Jørgensen (1994), amongst others, has advocated structurally dynamic models (models where parameters change according to a goal function) as the best way of capturing changes in species with changes in conditions. Without going to that extent, functional responses with the flexibility of the "ecosim-like" response used here, set within a multi-linked web, are also able to reflect the more dynamic changes that may occur within a web as ecosystem conditions change. However, given the high number of parameters biogeochemical models can require and that trends rather than specific quantitative values are usually sufficient for model interpretation and subsequent recommendations, "Holling-type" functional responses may still suffice. As stated above, this topic requires careful thought and should be a key part of any model formulation discussion.

One recommendation that can be made based on the results presented here is that research aimed at empirically determining the nature of functional responses in real systems is clearly needed. It is likely that, unlike the model presented here, in real systems different groups will have different types of functional responses. Furthermore, many bay ecosystems are changing and given the sensitivity of models like BM2 to the form of functional response used, there is a real need to properly establish the nature of

the functional responses in real systems (at least for some groups).

Model closure

Plankton modelers recognize that the form of model closure used requires careful consideration. While it is notable that the form of model closure does not have the dominating effect on the BM2 ecosystem model that it has on simpler plankton models (Steele and Henderson 1992, Edwards and Brindley 1999, Murray and Parslow 1999b, Edwards and Yool 2000), it was important nevertheless. Detailed bifurcation analysis, such as in Edwards and Brindley (1999), is not possible for a model of this size, so our conclusions must be based on the simulation runs. Previous papers on the subject (Steele and Henderson 1992, Edwards and Brindley 1999, Murray and Parslow 1999b, Edwards and Yool 2000) have concentrated on the steady-state stability status achieved when using different closure terms, while this paper has concentrated on the overall effects on model dynamics. Despite these differences, comparison of conclusions from the different works is instructive.

The necessity of including responsive top predators (either explicitly or implicitly via a quadratic mortality term) agrees with the general findings of the earlier studies. The change in behaviour of the run employing "no-linear" model closure under "baseline" conditions also gives some support for inclusion of separate natural mortality (linear) and higher predation (quadratic) terms. McGillicuddy et al. (1995), Murray and Parslow (1997) and Broström (1998) have successfully used this division of mortality terms, and the findings of Edwards and Brindley (1999) and Edwards and Yool (2000) do recommend it. However, Edwards and Brindley (1999) and Edwards and Yool (2000) caution that the use of both mortality terms requires the estimation of two (rather than one) poorly known parameter, which may mitigate against its use. Thus, given our results, the argument for the use of both terms is not overwhelming, and use of the

linear term may not be necessary. However, this may not be the case under oligotrophic conditions or extreme overfishing. In both of these cases the biomasses of many groups may be very low, which is precisely the situation in which quadratic mortality alone may yield unrealistic dynamics (Edwards and Brindley 1999). Further work to address this issue is required.

One final concern about model closure is whether or not the top predators must be included explicitly. A comparative analysis of the application of BM2, IGBEM and ECOSIM (Christensen and Pauly 1992, Walters et al. 1997) to Port Phillip Bay suggested that the implicit representation of the top predators (sharks, mammals and birds) in the biogeochemical models may not be capable of capturing some of the dynamics of that part of the web (chapter 7). This suggests that the top predators might need to be included explicitly, but the expansion of BM2 to explicitly represent the top predators did not see any substantial shifts in model behaviour. The clear indication is that unless the top predators are of particular concern in themselves (due to being a large component of the system, a conservation concern, or harvested group), their explicit inclusion in biogeochemical models is not required. Quadratic model closure appears to be acceptable regardless of the size of the web being considered.

6.5 Conclusions

Ecosystem models are one tool that has been advocated for ecosystem management (Walters et al. 1997, Sainsbury et al. 2000). Consequently, the impact of formulation decisions on their behaviour needs to be considered. Predation, in the form of grazing terms and model closure, is a crucial part of ecosystem models that incorporate ecology or biogeochemistry (Edwards and Yool 2000, Tett and Wilson 2000). The work discussed here indicates that, unless the top predators of a system are of particular interest, the additional complexity of their explicit inclusion can be avoided

by the use of a quadratic term for model closure. The use of a quadratic mortality term to close the model allows for realistic predictions across a range of conditions.

The specification of a suitable grazing term is more complex. Whereas linear plankton models have predicted that the grazing term has little real effect on model behaviour, our results for more complex webs indicate otherwise. Thus, careful consideration must be given to this part of the model formulation. There are biologically and mathematically sound arguments for including the more sophisticated dynamics of functional responses such as the "bounded", "dynamic" and "ecosim-like" responses trialled here (Bryant et al. 1995, Walters et al. 2000, Abrams and Linzburg 2000). However, given the extra detail and increased information required to parameterise and validate these formulations, a simpler "Holling-type" functional response may be sufficient. This is particularly true if preliminary studies or modelling exercises indicate that the "Holling-type" functional responses will lead to the same general conclusions and behaviour as more sophisticated functional responses. Nevertheless, some degree of sophistication is required in the functional response employed as the simple application of a "type I" response is unlikely to be useful under changing ecosystem conditions (e.g. increasing nutrient loads or fishing pressure). It is doubtful that any one functional response will be suitable for all groups, models and environments. The demonstration here, that model behaviour can be sensitive to the form of the grazing terms used, shows that efforts to empirically determine the form of functional responses in real systems are warranted. Along with the topology and the form of the trophic web that defines the framework of the model, the grazing terms are a feature that require particularly careful consideration during the conceptualisation and development of ecosystem models.

Chapter 7 Lessons learnt from the comparison of three ecosystem models for Port Phillip Bay, Australia

Abstract

Three ecosystem models were tuned to data from Port Phillip Bay, Australia. Several general conclusions can be drawn by comparing predictions of the three models across a range of fishery management strategies and scenarios for environmental change. First, the large, shallow and enclosed physical structure of Port Phillip Bay and the dependency of many fish groups on spawning stocks from outside the immediate area may see the bay react more strongly to eutrophication than to fishing. Second, a selected set of indicator groups (in this case, sharks, seagrass and chlorophyll a) seems to capture the major ecosystem impacts of alternative management scenarios, whether the biomass and productivity of important groups declines, persists or increases. This has obvious implications for system monitoring in an adaptive management approach. Third, multispecies or ecosystem models can identify potential impacts that a series of single species models cannot, such as non-intuitive changes in biomass when species interactions outweigh fishery induced pressures. Finally, policies that focus on protection of species or groups only at higher trophic levels can fail to achieve sensible ecosystem objectives and may push systems into states that are far from pristine.

Keywords

biogeochemical, ecosystem, model, ECOSIM, ECOPATH, Port Phillip Bay

Note: This chapter resulted from work undertaken at an ECOPATH with ECOSIM workshop on the use of ecosystem models to investigate multispecies management strategies for capture fisheries held at the University of British Columbia, Vancouver

Canada, in July 2000. The work involved fitting the models to the current conditions of Port Phillip Bay and then considering the potential effects of management strategies. As a result, some of the terminology used in this chapter differs from that used in the rest of the thesis. Most importantly, whereas the term "standard run" is used to refer to the default run of the full models in all the other chapters the term "base case" is used here. Further, whereas "baseline" is used to refer to the default nutrient loadings and fishing pressures in all the other chapters the terms "current conditions" or "*status quo*" are used in this chapter. I apologise for any confusion this may cause.

7.1 Introduction

Concern over sustainable and responsible management of ecosystems, rather than particular species of interest, has grown over the last century, and particularly within the last decade. This is reflected in the increasing adoption in international treaties and national legislation of policies that take explicit account of such concerns. For example, Australia has adopted a national oceans policy that requires, *inter alia*, development of regional marine plans based upon principles of ecosystem management. Despite this level of interest and activity, the scientific and management tools to underpin such policies are poorly developed. In particular, the tools to predict the impact of alternative uses and management strategies are still being developed (Sainsbury et al. 2000). In the context of ecosystem management, the use of trophic models has been proposed to predict such impacts (Walters et al. 1997, Walters et al. 1999). A range of such models has been developed, but to date there has been little effort to compare and contrast such models, or to compare their strengths and weaknesses (Baretta et al. 1994, Baretta et al. 1996, this thesis).

In this study, three separate ecosystem models are used to explore the utility of such models for the assessment of potential management strategies and their likely

consequences. These three models span a range of process detail, from ECOSIM with its relatively compact formulation (Christensen et al. 2000), to the more nutrient-oriented Bay Model 2 (BM2) (chapter 2), and finally to a highly detailed process model, the Integrated Generic Bay Ecosystem Model (IGBEM) (chapter 1). Between them, these three models reflect much of the range of detail found in simulation models currently being built and used to understand and predict the ecosystem effects of fishing and eutrophication. Unfortunately, their respective histories and the varying purposes for which they were developed mean that the models do differ in many ways and that there is no systematic variation in assumptions. This can make extraction of organising principles or conclusions difficult. However, there is value in determining whether various existing ecosystem models of different forms predict similar outcomes in response to changing conditions and management policies. This kind of information can be instructive with regard to understanding the implications of the formulations used and whether results are robust across modelling methodologies.

The real world system used as the data source and guide for this model comparison is Port Phillip Bay (PBB), adjacent to Melbourne, Australia. During the 160 years since European settlement, PPB has come under increasing pressure from nutrient enrichment and fisheries exploitation. Approximately 15% of Australia's population live within the catchment area of PPB, and the bay has become the focal point for many of their recreational pursuits. It has been estimated that the annual recreational effort is around 670,000 angler hours, which results in the landing of about 470t of fish (Anon 1997). The bay's commercial finfish fisheries land over 60 species, with a total annual take of between 700 and 2000t worth about $3 million AUD wholesale. A number of invertebrate species are also landed, though many only opportunistically as bycatch. The main targeted invertebrate harvests are cultured mussels and wild abalone, with annual landings of 600t worth $1.5 million AUD and 50t worth $1 million AUD

respectively. Until the late 1990s scallops were the most intensively harvested and valuable fishery in PPB, with up to 10,000t (shell weight) being landed per year. However, the fishery was highly variable (fluctuating by two orders of magnitude in 3 years) and the sediment plumes associated with the dredges used in the fishery led to public concern. The fishery was closed in 1997.

PPB is a relatively "easy" system to model as it is a shallow and nearly enclosed temperate bay. It has an area of approximately 1930 km^2, mostly of waters less than 8m deep, though it reaches 24m at its deepest points. With only 8 drainage basins feeding the bay, and a large sand bar delta and narrow seaward opening restricting exchange with Bass Strait, it has minimal boundary condition problems. The bay has also been the subject of a number of quite extensive environment studies, one or more per decade since the late 1940s, and so there is a large amount of good quality information available for use in model construction and validation (Harris et al. 1996).

Eutrophication and fishing are the two most significant anthropogenic impacts on PPB. The difficulties inherent in interpreting and managing the consequences of human actions on marine systems have meant that fisheries and nutrient related concerns have traditionally been dealt with separately. This is not just the case for Australian bays and near shore waters, but is commonplace worldwide. However, there is increasing evidence that primary productivity and fisheries are more tightly linked than previously thought (Houde and Rutherford 1993, Nielsen and Richardson 1996). With this in mind, the three models are compared across a range of levels of fishing pressure and nutrient inputs.

7.2 Methods

7.2.A Model Descriptions

A brief description of the general form of each model is given below, but space precludes an extended discussion of each of their features, structures and assumptions. To allow for an informed comparison, the essential details of the models and how they vary are listed in Table 7.1. Further, to give some idea of the degree of variation in process detail between the models, the formulation for phytoplankton production is given in Table 7.2. This example is a fair representation of the difference in formulation detail for the lower trophic levels. However at the highest levels, especially those where split pools (juvenile and adults) are included in ECOSIM, the detail can swing back more the other way. At these levels all the models include age structure, explicit recruitment and split food intake into portions allocated to growth and reproduction, though the exact method of doing this does vary between models (Christensen et al. 2000, chapters 1 and 2).

The variation in process detail between the models is one of the motivating forces for the comparison of the models and their predictions. However, other major differences in underlying model assumptions must be kept in mind in comparing the models and their dynamics. These include:

(a) the consumption formulations (a forage arena approach is used in ECOSIM, but Holling Type functional responses are used in the other two models),

(b) the lack of bycatch in the standard versions of IGBEM and BM2,

(c) the omission of invertebrate fisheries from IGBEM,

(d) the absence of explicit spatial structure in ECOSIM

(e) the static nature of the birds, mammals and sharks in BM2 and IGBEM and

(f) the stock structure of the fish groups with its inherent implications for the form of the stock-recruit relationship used.

Table 7.1: Comparison of the underlying structure and assumptions of the three ecosystem models, ECOSIM, IGBEM and BM2. The standard set-ups used for the runs in this study are given, any feature where alternatives may be implemented are marked with a *.

	Model		
Feature	**ECOSIM**	**BM2**	**IGBEM**
General features			
Biomass units	t/km2 (wet weight)	mg N/m3 (dry weight)	mg/m3 of C, N, P, Si (dry weight)
Input forcing	yes (of primary producers), interannual	yes (of nutrients and physics), interannual, seasonal, tidal	yes (of nutrients and physics), interannual, seasonal, tidal
Level of group detail	variable (age group of species up to entire trophic levels)	functional group	functional group
Formulation related			
Consumption formulation	forage arena	type II*	mixed (type II, type III)
Formulation detail	simple (expansion of ECOPATH master equation)	general (growth, mortality, excretion explicit)	physiological (assimilation, basal/ activity/stress respiration, defecation, excretion, ingestion, mortality all explicit)
Light limitation	no	optimal irradiance fixed	phytoplankton can adapt to changes in ambient light levels
Mixotrophy	no (no mixed consumers-producers defined in the ECOPATH model)	yes (Dinoflagellates)*	no
Nutrient limitation	no	yes (external)	yes (internal)
Nutrient ratio	-	Redfield	internal nutrient ratio
Oxygen limitation	no	yes	yes
Sediment burial	no	no	yes*
Sediment chemistry	no	yes (dynamic, with sediment bacteria)	yes (empirical, sediment bacteria are a tracer only)
Shading of primary producers	no	yes	yes

Table 7.1: Continued

	Model		
Feature	**ECOSIM**	**BM2**	**IGBEM**
Spatial structure	no explicit spatial structure (ECOSPACE model not considered here)	explicit (8 and 59 box versions)*	explicit (8 and 59 box versions)*
Temperature dependency	no	yes	yes
Model closure			
Status of birds	dynamic	static loss term on fish only	static loss term on fish only
Status of mammals	dynamic	static loss term on fish only	static loss term on fish only
Status of sharks	dynamic	static loss term on fish only	static loss term on fish only
Fish and fisheries related			
Age structured fish	yes (juvenile + adult)	yes (9 age classes)	yes (9 age classes)
Fishery Discards	target and bycatch species	target species only*	target species only
Invertebrate fisheries	yes	yes	no ('fix' implemented by adjusting the mortality terms of the groups concerned)
Stock-recruit relationship	dynamic	constant recruitment	constant recruitment
Stock structure	self-seeding (entire stock in the bay)	external (reproductive stock outside the bay produces the recruits, oldest age classes migrate out of the bay to join this stock)	external (reproductive stock outside the bay produces the recruits, oldest age classes migrate out of the bay to join this stock)

Table 7.2: Process detail involved in the phytoplankton production for each model.

ECOSIM	BM2	IGBEM
$= \frac{r \cdot B}{1 + B \cdot h}$ where B = Biomass of the phytoplankton r = the maximum P/B ratio that can be realised (at low B) and $\frac{r}{h}$ = the maximum net primary production when the biomass is not limiting to production (at high B)	$= \mu \cdot \delta_{irr} \cdot \delta_N \cdot B$ where B = Biomass (mg N m^{-3}) of the phytoplankton group (4 types) μ = maximum temperature dependent growth rate δ_N = nutrient limitation factor $= \frac{DIN}{\kappa_N + DIN}$ and DIN = Ammonia + Nitrate unless also limited by Silica (Si) then $= \boldsymbol{min}\left(\frac{DIN}{\kappa_N + DIN}, \frac{Si}{\kappa_{Si} + Si}\right)$ κ_{XX} = is the half saturation constant for the uptake of the nutrient XX δ_{irr} = light limitation factor $= \boldsymbol{min}\left(\frac{IRR}{\kappa_{irr}}, 1\right)$ IRR = Light κ_{irr} = is the half saturation constant for the uptake light	$= \mu \cdot \delta_{irr} \cdot \delta_{Nut} \cdot B_C$ where B_C = Biomass (mg C m^{-3}) of the phytoplankton group (4 types)** μ = maximum temperature dependent growth rate δ_{Nut} = nutrient limitation factor $= \boldsymbol{min}(\delta_N, \delta_P)$ $\delta_N = \boldsymbol{min}\left(1, \boldsymbol{max}\left(0, \frac{B_C - \beta_{CNlow}}{\beta_{CN\,int} - \beta_{CNlow}}\right)\right)$ $\delta_P = \boldsymbol{min}\left(1, \boldsymbol{max}\left(0, \frac{B_C - \beta_{CPlow}}{\beta_{CP\,int} - \beta_{CPlow}}\right)\right)$ β_{CXXlow} = minimum permissible nutrient ratio of C:XX for the cell β_{CXXlow} = standard internal nutrient ratio of C:XX for the cell unless also limited by Silica (si) then $= \boldsymbol{min}\left(\boldsymbol{min}(\delta_N, \delta_P), \boldsymbol{min}\left(1, \frac{Si}{2 \cdot \kappa_{Si}}\right)\right)$ δ_{irr} = light limitation factor $= \boldsymbol{min}\left(1, \frac{IRR}{\kappa_{irr\_adjusted}}\right)$ IRR = Light κ_{irr} = is the half saturation constant for the uptake light adjusted for acclimation to new ambient light conditions

** There are also N and P pools of the biomass explicit in IGBEM and the production in these is based on the internal nutrient ratio and the production for the B_C pool.

These assumptions are identified as having the most potential to cause differences in model outcome. The assumptions relating to bycatch, invertebrate fisheries, static top predators and the form of the stock structure and recruitment relationship are likely to affect the higher trophic levels (the fish in particular). More generally, consumption (predation) and spatial structure have been major research topics in theoretical ecology for a large part of the past century, and have been found to have significant effects in other ecological model studies. For example Hassell and May (1973) and Holmes et al. (1994) have shown that, for predator-prey and competition models, different forms of the consumption formulation, or the addition of spatial structure, can lead to very different sets of population behaviour and species interactions. In some ways it is unfortunate that so many factors vary at once between the three models being considered. However only the ECOPATH with ECOSIM model presented here was built explicitly for PPB. The other two models were built as part of a more general and theoretical study of ecosystem models (this thesis) and then tuned to data from PPB to allow for the comparisons considered here.

IGBEM was created by tying together two existing models, the Port Phillip Bay Integrated Model (PPBIM) (Murray and Parslow 1997, 1999a) and the European Regional Seas Ecosystem Model II (ERSEM II) (Baretta et al. 1995, Baretta-Bekker and Baretta 1997). The biological groups from ERSEM II, as well as a few additional groups formulated in the same way, were tied into the physical and biogeochemical submodels of PPBIM (chapter 1). In its final form, IGBEM is a highly physiologically based process model, which tracks the carbon, nitrogen, phosphorus and silicon pools of 7 primary producer groups (3 benthic, 4 planktonic), 4 zooplankton groups, 3 infaunal groups, 3 epifaunal groups and 4 fish groups (Figure 7.1). This is done within a spatial geometry of 59 polygons (boxes) which parallel the geographical form of PPB, with the size of the polygons reflecting the speed with which physical variables change within

Figure 7.1: Schematic diagram showing the groups in BM2 and IGBEM and their relative trophic positions. The bacterial groups are omitted from the diagram and the model comparisons as no equivalent group exists in the ECOPATH model. The greyed box indicates the position of the dinoflagellates when mixotrophy was allowed in BM2. The dashed boxes indicate the position of the static predator groups implemented for the nutrient model runs used here. Groups marked with a # are fished explicitly in IGBEM and those marked with a * are fished in BM2.

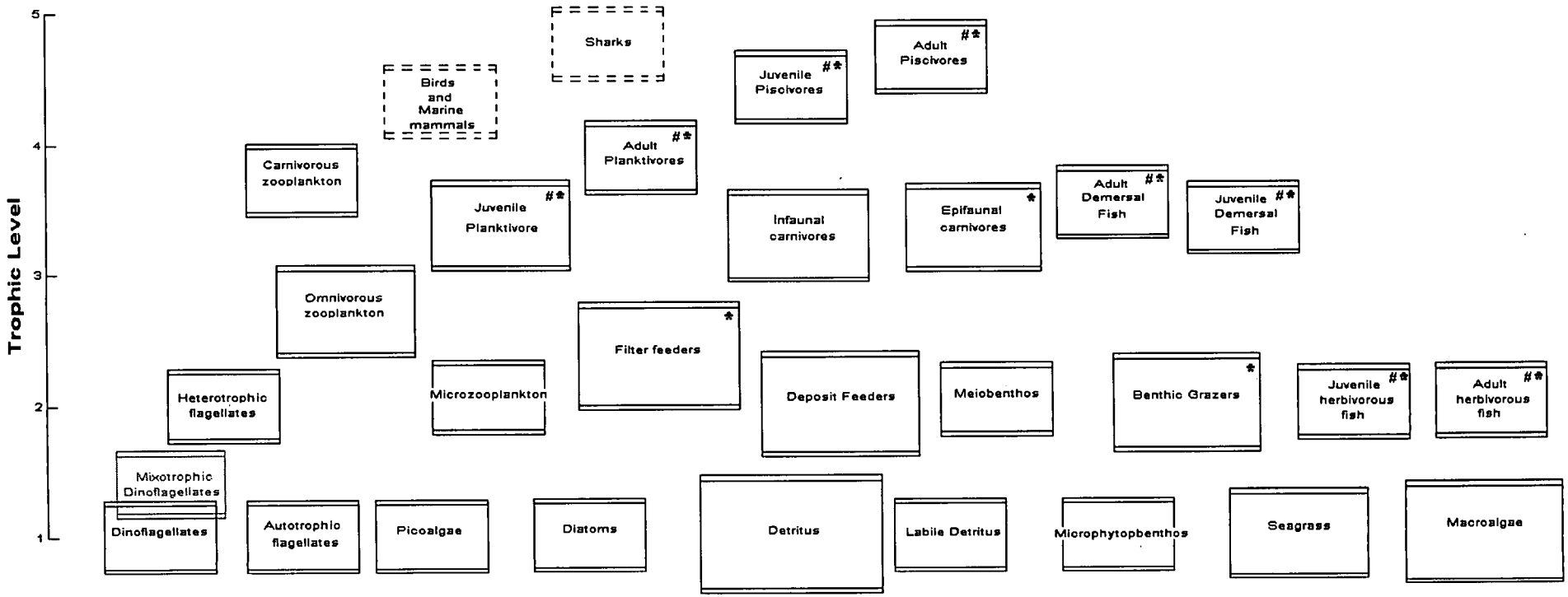
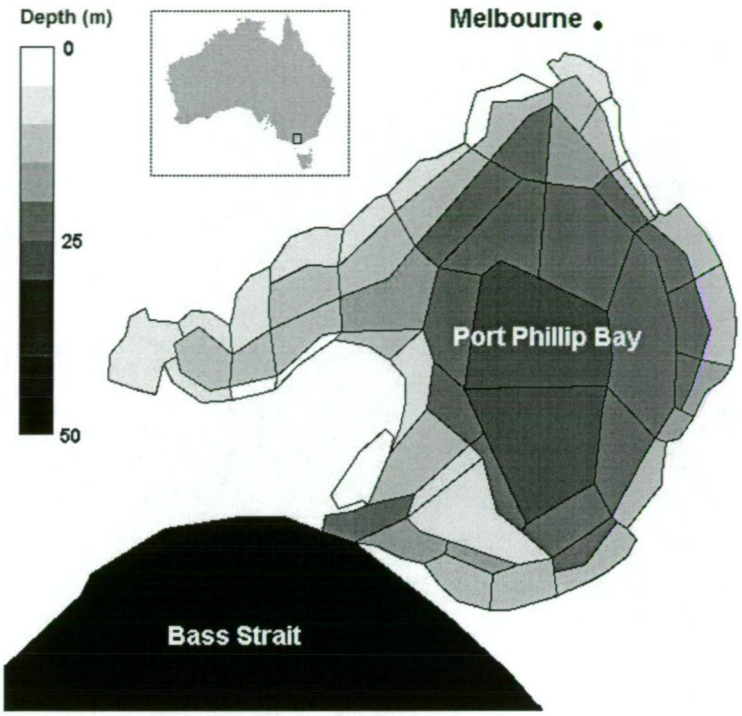


Figure 7.2: Depth map of Port Phillip Bay, Melbourne, Australia. The inset map of Australia indicates the location of Port Phillip Bay. The polygons marked on the large map are those of the standard 60 box geometry used for BM2 and IGBEM.



that part of the bay (Figure 7.2). The level of detail included in this model is considered to be at the upper level, but not beyond, that which is employed in ecosystem models currently in use (e.g SSEM (Sekine et al. 1991), ERSEM II (Baretta-Bekker and Baretta 1997) and ATLSS (DeAngelis et al. 1998)).

BM2 has the same trophic groups, general submodels (water column, sediment, epibenthic) and physical (transport, mixing and spatial geometry) details as IGBEM. BM2 does not have sediment burial, but does have dinoflagellate mixotrophy, while IGBEM has the reverse. The greatest difference between IGBEM and BM2 lies in the level of process detail. BM2 is an order of magnitude simpler, with very similar dynamical representation to PPBIM (Murray and Parslow 1997, 1999a). Processes such as excretion and respiration are not modelled explicitly, but are subsumed into

generalised assimilation and waste production equations (chapter 2). Further, BM2 only models the nitrogen component, and relies on Redfield ratios, rather than internal nutrient ratios, to determine the form of nutrient dependent activities. This level of detail is more representative of the most commonly utilised eutrophication and water column trophic models (Fransz et al. 1991).

Data from the Port Phillip Bay Environmental Study (PPBES), primarily for the years 1994 – 1995, were used to calibrate IGBEM and BM2 to achieve a satisfactory representation of the biological conditions in PPB (in mg N m^{-3}). In a few instances it was necessary to draw values from the general literature or use data from other years to fill in gaps, but this was kept to a minimum. The same data were then used to construct an ECOPATH model, converting from mg N m^{-3} to t km^{-2} wet weight under the assumption that N makes up 1% of an organism's wet weight. The resulting model contains one phytoplankton group, small and large zooplankton groups, 9 benthic invertebrate groups, 3 benthic primary producers, 16 fish groups (some of which were species split into juvenile and adult groups), marine mammals, birds and detritus. While the level of aggregation of species in the ECOPATH model does not match that in BM2 and IGBEM, it is felt that it was better suited to, and more typical of, what is usually found in ECOPATH models. Moreover some of the group splitting was necessary to avoid high levels of cannibalism, though this is not possible for the zooplankton or piscivore groups due to a lack of relevant information. The identity of the various groups and the value and source of the input parameters for the ECOPATH model are given in Table 7.3 and a schematic diagram of the system in Figure 7.3. Eight harvesting enterprises are also included in the model. These are the purse seine, scallop dredge, haul seine, longline, mesh net, dive and pot fisheries as well as the culture of mussels (details summarised in Table 7.4). There is not enough information to specify a separate recreational fishery, so the recreational catches are aggregated with those for

Table 7.3: The basic input parameters for the Port Phillip Bay ECOPATH model. All values shown are those of the final balanced model, but changes made during balancing are noted. In addition the original P/B and Q/B for pilchards are halved and all those for all other fish (juvenile snapper down to rays) were quartered during balancing. Those columns marked by * were calculated by ECOPATH. The TS values stated are the correction values used to correct the trawl data to give total biomass estimates for that group.

Group name	Group description	Habitat area	B (t/km²)	P / B (/yr)	Q / B (/yr)	Unassim Q	EE*	P/Q*	Catch (t/km2 /yr)	Discards (t/km2/ yr)	Notes on Balancing	References
Phytoplankton	Lumped phytoplankton	1	7.617	250	-	-	0.604	-	0	0	P/B increased 15%	Murray and Parslow, 1997
Small zooplankton	Zooflagellates and small copepods	1	6.477	36.8	59.781	0.3	0.713	0.616	0	0	Q/B increased 32%.	Beattie et al. 1996 Holloway and Jenkins 1993
Large zooplankton	Mesozooplankton	1	9.974	23.8	38.609	0.3	0.866	0.616	0	0	Q/B increased 32%	Beattie et al. 1996 (Q/B, B) Holloway and Jenkins 1993 (P/B)
Deposit feeders	Sediment eating invertebrates	0.835	69.948	4.8	66.7	0.3	0.73	0.072	0	0	B decreased 40%	Poore 1992 Wilson et al. 1993
Scallops and mussels	Wild scallops and cultured mussels	0.835	4.922	3.1	10.9	0.3	0.25	0.284	0.862	0.25	B decreased 10%	Kailola et al. 1993 Poore 1992 Wilson et al. 1993
Filter feeders	Non commercial filter feeders (including oysters)	0.85	73.511	2.8	11.8	0.3	0.756	0.237	0	0.025	B decreased 35%	Poore 1992 Wilson et al. 1993
Infaunal predators	Burrowing worms and other predatory infauna	0.4	13.575	5.4	58.4	0.2	0.999	0.092	0	0	B decreased 20%	As for filter feeders
Epifaunal predators	Crustaceans, gastropods and starfish.	0.4	2.363	2.9	21.9	0.2	0.978	0.132	0	0.026	B decreased 10%	As for filter feeders
Southern rock lobster		0.37	0.068	0.73	12.41	0.2	0.874	0.059	0.003	0	B decreased 2%	Anon 1996 Wilson et al. 1993
Abalone	Green and black lip abalone	0.37	0.699	0.73	12.41	0.3	0.994	0.059	0.048	0	B decreased 2%	Anon 1996 Poore 1992 Wilson et al. 1993

Table 7.3: Continued

Group name	Group description	Habitat area	B (t/km²)	P / B (/yr)	Q / B (/yr)	Unassim Q	EE*	P/Q*	Catch (t/km2 /yr)	Discards (t/km2/ yr)	Notes on Balancing	References
Other grazers	All other grazers, only urchins fished.	0.4	2.249	0.88	11.68	0.3	0.758	0.075	0	0	B decreased 10%	Anon 1996 Kailola et al. 1993 Poore 1992 Wilson et al. 1993
Scavengers	All epifauna opportunistic scavenging feeders	0.4	9.326	6.86	55.48	0.25	0.834	0.124	0	0	B decreased 10%	Poore 1992 Wilson et al. 1993
Microphytobenthos		1	18.135	44	-	-	0.14	-	0	0	P/B increased 25%	Murray and Parslow 1997
Seagrass		0.1	2.591	24	-	-	0.345	-	0	0.01	P/B increased 25%	As for microphytobenthos
Macroalgae		0.7	25.907	20	-	-	0.301	-	0	0.01	P/B increased 25%	As for microphytobenthos
Clupeoids	Pilchards, anchovy and sprat.	1	2.85	1.15	30.15	0.2	0.993	0.038	0.812	0	P/B and Q/B decreased 50%	Anon 1996 Hall 1992 Parry et al. 1995
Juvenile snapper	<3 yrs. VBGF k = 0.1079, Wavg/Wk = 1.16	0.7	0.469	0.548	2.737	0.2	0.973	0.2	0.012	0	P/B and Q/B decreased 75%	Officer and Parry 1996 Parry et al. 1995 Gunthorpe et al. 1997
Snapper	3+ yrs (splits based on recruitment to fishery and 50% maturity)	0.7	0.376	0.493	2.737	0.2	0.785	0.18	0.033	0.001	P/B and Q/B decreased 75%	As for juvenile snapper
Juvenile flatfish	<3 yrs. VBGF k = 0.19, Wavg/Wk = 1.2	0.75	2.319	0.821	2.737	0.2	0.977	0.3	0.004	0.001	P/B and Q/B decreased 75%	As for juvenile snapper
Flatfish	3+ yrs	0.75	2.285	0.411	2.737	0.2	0.902	0.15	0.143	0.011	P/B and Q/B decreased 75%	As for juvenile snapper
Juvenile KG whiting	<3 yrs. VBGF k = 0.16, Wavg/Wk = 1.1. TS = 5	0.8	0.142	0.821	2.737	0.2	0.936	0.3	0.06	0	P/B and Q/B decreased 75%	As for juvenile snapper
KG whiting	3+ yrs. TS = 5	0.8	0.117	0.548	2.737	0.2	0.293	0.2	0.001	0	P/B and Q/B decreased 75%	As for juvenile snapper
Juvenile piscivores	<3 yrs. VBGF k = 0.42, Wavg/Wk = 1.1. TS = 20	0.72	0.567	0.821	2.737	0.2	0.999	0.3	0	0	P/B and Q/B decreased 75%	As for juvenile snapper
Piscivores	3+ yrs. TS = 20	0.72	0.288	0.411	2.737	0.2	0.92	0.15	0.001	0	P/B and Q/B decreased 75%	As for juvenile snapper

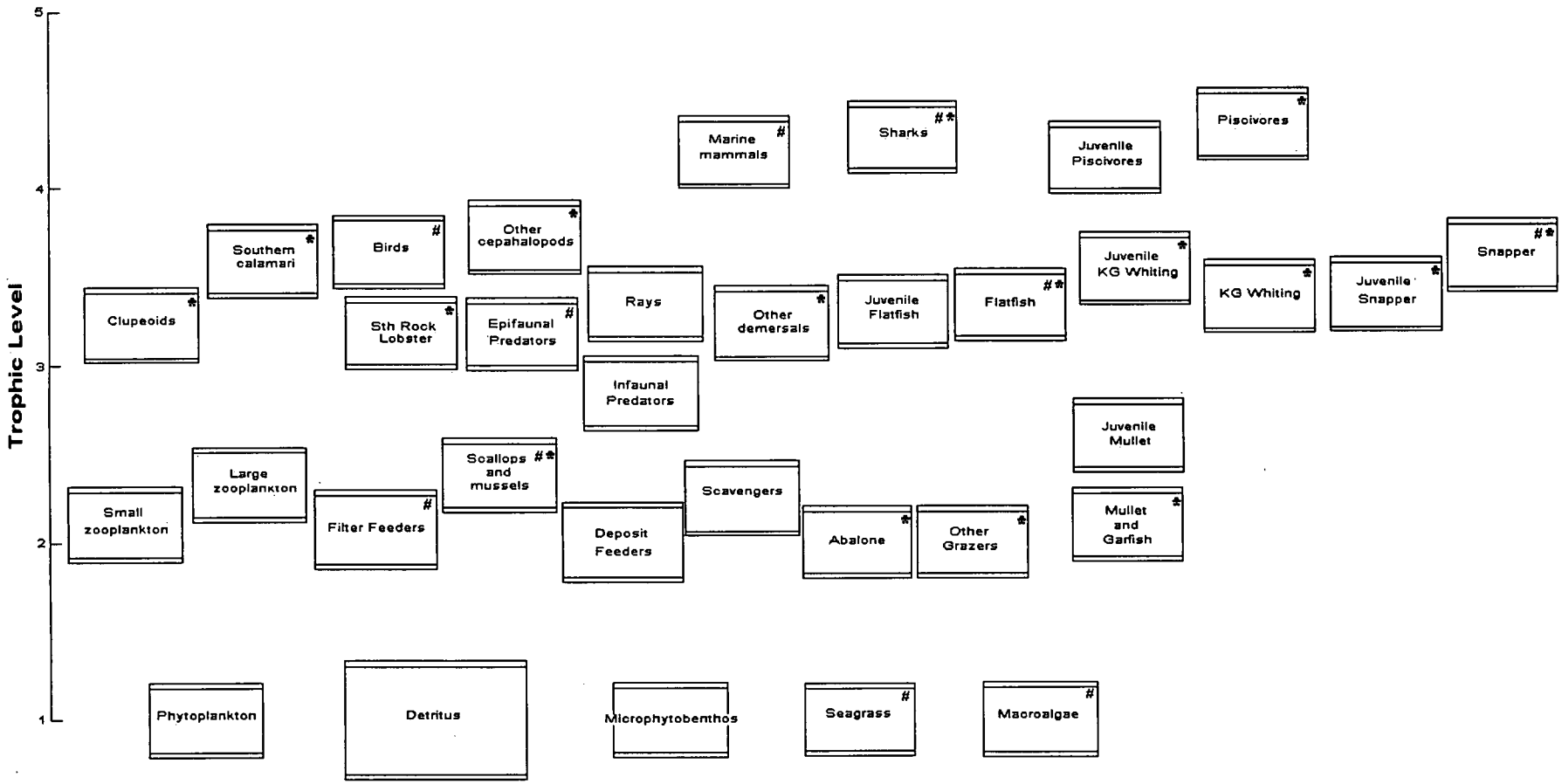
Table 7.3: Continued

Group name	Group description	Habitat area	B (t/km²)	P / B (/yr)	Q / B (/yr)	Unassim Q	EE*	P/Q*	Catch (t/km2 /yr)	Discards (t/km2/ yr)	Notes on Balancing	References
Juvenile mullet	<3 yrs. VBGF k = 0.271, Wavg/Wk = 1.15. TS = 4.45	0.825	0.526	0.411	2.737	0.3	0.993	0.15	0	0	P/B and Q/B decreased 75%	As for juvenile snapper
Mullet and garfish	3+ yrs. TS = 4.45	0.825	0.383	0.329	2.737	0.3	0.909	0.12	0.053	0	P/B and Q/B decreased 75%	As for juvenile snapper
Other demersals	All other demersal finfish. TS = 2	0.965	4.899	0.548	2.737	0.2	0.849	0.2	0.041	0	P/B and Q/B decreased 75%	As for juvenile snapper
Southern calamari	TS = 4	0.93	0.319	1.825	18.25	0.2	0.785	0.1	0.05	0		Officer and Parry 1996 Parry et al. 1995 Gunthorpe et al. 1997 Lee 1994
Other cephalopods	Octopus. TS = 4	0.945	0.415	1.369	9.125	0.2	0.952	0.15	0	0		As for southern calamari
Rays		0.9	6.166	0.234	1.56	0.2	0.007	0.15	0	0	P/B and Q/B decreased 75%	Officer and Parry 1996 Parry et al. 1995 Gunthorpe et al. 1997 Schmid et al. 1993
Sharks	To get B used demersal trawl data, TS = 13.35.	0.62	0.148	0.234	1.56	0.2	0.639	0.15	0.002	0.001		As for rays
Birds	Shorebirds (based on representative densities of shorebirds in similar habitats elsewhere)	1	1.018	0.07	1.69	0.2	0.145	0.041	0	0		Briggs et al. 1997 PICES 1998
Marine mammals	Dolphins and seals	1	0.02	0.09	19.88	0.2	0.006	0.005	0	0		Dolphin Research Institute 2000
Detritus	Biomass represents top 20cm of sediment. 398.96 t imported per yr.	1	14766.84	-	-	-	0.994	-	0	0		Nicholson et al. 1996 Harris et al. 1996

Table 7.4: Landings, discard and total value information for the harvest methods included in the Port Phillip Bay ECOPATH model.

Fishery	Target Species	Bycatch Species	Landings (t/km2/yr)	Discards (t/km2/yr)	Value ($AUD)
Purse seine	Clupeoids		0.812	0	1,500,000
Scallop dredge	Scallops	Scallops Filter feeders Epifaunal predators Seagrass Macroalgae Flatfish	0.551	0.3205	8,000,000
Haul seine	Juvenile and adult King George whiting Mullet and garfish Southern calamari Other cephalopods	Snapper	0.1639	0.001	930,000
Longline	Juvenile and adult snapper	Juvenile and adult flatfish Sharks	0.041	0.012	500,000
Mesh nets	Juvenile and adult snapper Juvenile and adult flatfish Piscivores Other demersals Sharks	Marine mammals	0.1945	0.00001	780,000
Dive	Abalone Other grazers	Epifaunal predators	0.0483	0.0005	1,175,000
Aquaculture	Mussels		0.311	0	1,500,000
Pot	Southern rock lobster		0.003	0	125,000

Figure 7.3: Schematic diagram of the Port Phillip Bay ECOPATH model, showing the constituent groups and their relative trophic positions. Groups marked with a * are landed by fisheries included in the model, whereas groups marked with a # are species that are taken and discarded.



the commercial fishery using the same gear. As with all ECOPATH models some balancing is required. This process involved adjusting some, ideally the most uncertain, of the diet compositions, biomasses and the Production/Biomass ratios (P/B) and Consumption/Biomass ratios (Q/B) input until all of the ecotrophic efficiencies are less than 1 and the gross food conversion efficiencies are within sensible bounds for each group. However all parameter values remain within the ranges given in the PPBES technical reports (though many are moved from the centre to one end or the other of the quoted ranges). The biomass of the deposit feeders proves to be a critical value in the model, but this is also one of the most uncertain.

In hindsight a potentially confounding issue arises from the fact the nutrient models (IGBEM and BM2) are calibrated, while the ECOPATH model undergoes balancing. The nutrient models are calibrated by setting their parameters (growth, mortality etc) based on the species composition of PPB and then minor adjustments are made to these so that the biomass levels output are reasonable reflections of those reported in the PPBES technical reports. While the biomasses from the technical reports are also used in the ECOPATH model they undergo some significant changes during balancing. Thus the biomass values in the final version of the ECOPATH model no longer match those used to calibrate the nutrient models. (While not cripplingly important for all groups in the model, it became obvious that in an ideal situation more tuning would have been beneficial in spots and these will be identified in the following discussion.)

When the ECOPATH model is extended into an ECOSIM model, a mediation effect is added, to reflect the critical importance of seagrass to juvenile King George whiting. This does not have a deleterious impact on model stability and behaviour. As the vulnerability settings used in an ECOSIM model can be crucial (Christensen et al. 2000), alternative sets of vulnerabilities are tested. To avoid confusion with the term

vulnerability as used in fisheries science, the ECOSIM vulnerabilties are referred to as "refuge parameters" for the remainder of this chapter. In setting the refuge parameters for the fished groups estimates of virgin levels of egg production are used to give initial estimates of the refuge parameters and then these are adjusted slightly to obtain stable equilibria (no inherent rate of increase or decline) under *status quo* fishing mortalities (Fs). Refuge parameters for all groups are set at 0.5 with the following exceptions. Scallops, abalone, clupeoids, and both piscivore age classes are at lower levels (0.48, 0.45, 0.45, 0.4 and 0.4 respectively) while southern rock lobster, juvenile snapper, marine mammals and both King George whiting groups are at higher levels (0.8, 0.6, 0.9, 0.8 and 0.8 respectively).

IGBEM and BM2 are spatially explicit models, but an ECOSPACE form of the ECOSIM model for PPB has not been fully developed. Consequently, the final four years of the 20 year runs from IGBEM and BM2 are spatially averaged to give values for the entire bay and these are then used in the comparisons discussed here. The biomass units used in the internal model calculations of the three models also differ, so all biomasses have been converted to t/km2 to facilitate comparisons. Despite this, BM2 and IGBEM are referred to as nutrient models (as they deal with nutrient pools rather than total biomasses).

7.2.B Comparison of the three models

Once tuned to the data for PPB, the comparison of the three models and the potential management strategies was undertaken in a multi-step process. The following is an outline of the overall process, with each step briefly outlined in its own subsection.

This multi-step process allows for the clearest grasp of the individual and combined changes in the systems due to the effects of anthropogenically induced change in nutrient load and fish mortality and management intervention to do with these

factors. Base cases are compared first so that differences in the models when there is no change, or simple changes, can be understood before the more complex interaction of optimal and changing management strategies are applied.

7.2.B.1 Comparison of the "base case" results

Comparison of biomasses and Comparison of P/B and Q/B ratios

The spatially averaged output of the nutrient models is compared to the values used to construct the balanced ECOPATH model. As mentioned above, the Biomass (B), Production/Biomass (P/B ≈ Total mortality) and Consumption/Biomass (Q/B) values used in the ECOPATH model came from estimates reported in the PPBES. In contrast, the Biomass, P/B and Q/B values produced by the nutrient models are the outcome of tuning the physiological and process parameters to represent the species of PPB. Thus, there is uncertainty associated with the values produced by all three models. However, a model comparison is easier if there is an identifiable baseline to compare against and the easiest way of doing this is to designate one of the three models as that baseline. Moreover, the work presented here was done in the context of a larger evaluation of ECOSIM as a tool for considering the effect of fisheries policy. As a consequence, it was decided that the ECOPATH values are as good a baseline as any and so the nutrient models are measured against them. Ideally, all three models should be compared to an independent data set for the bay, but this is not possible at this time.

System-level indices

A comparison of the biomass, P/B and Q/B values provides only a partial summary of how well each model captures the overall state of the system. Production, consumption, biomass and catch results for each group are output routinely by the nutrient models and estimates of these values exist for PPB (the same data used to

construct the ECOPATH model). It is possible, therefore, to calculate an extended list of system-level indicators for the "base case" of each model. Unfortunately, this is not so easily done for any of the later simulation runs. Thus, only Mean Trophic Level (for the entire system), Mean Trophic Level for the Catch (including bycatch groups) and Total System Biomass are presented for these later runs.

Temporal dynamics

An important validation of simulation models is how well temporal dynamics are captured. Overall averages may be close, but this can conceal quite large phase lags and mismatches in the patterns produced through time by the models. Therefore, the temporal dynamics of biomass for each of the models is compared.

Alternative forcing scenarios

The models are compared under alternative nutrient and fishing mortality regimes. The regimes examined included:

- increase in nutrients (fivefold increase on current levels)
- decrease in nutrients (decrease to a fifth of current levels)
- increase in fishing mortality (across the board fivefold increase on current levels)
- decrease in fishing mortality (across the board reduction to a fifth of current levels)

The various regimes all represent longterm gradual change and are implemented in ECOSIM by taking the nutrient input files used to force IGBEM and BM2 and using them to force the phytoplankton and macrophyte groups in the ECOSIM model. Changes in F are sketched into the ECOSIM model directly via the scribble pad provided in the software (Christensen et al. 2000). The level of change implemented in

the scenarios is not an arbitrary choice. A fivefold increase in nutrients is known to cause eutrophication in the Port Phillip Bay Integrated Model (Murray and Parslow 1999a), and fivefold changes in F have not been uncommon during the history of some of the PPB fisheries.

Summary of conclusions for "base case" results

A summary of the major findings are presented from the "base case" runs before any fisheries policy analysis is implemented.

7.2.B.2 Fishing policy analysis

ECOSIM, with no change in nutrient load

The open and closed loop policy analysis option in ECOSIM is used to find optimal fishing strategies under a number of economic, social and ecological criteria (defined in Table 7.5).

"Optimal" policies implemented in BM2 and IGBEM, with no change in nutrient load

The optimal policies derived in ECOSIM are trialed in IGBEM and BM2 to see what effects are produced in these models.

Change in F scenarios vs the results of the optimisations

As the optimisation with an economically weighted objective function produces an increase in most Fs and the optimisation with an ecologically weighted objective function produces a general drop in Fs, another comparison is possible. The changes in biomass that result from the scenarios where there are across the board changes in F are compared with the results of the optimisations.

Fishing policy analysis by ECOSIM, with a change in nutrients

The optimisation process is repeated for those cases where there is a long-term change in nutrients. As the nutrients (and thus productivity) undergo large changes with time, a single F applied for the entire period is unlikely to be optimal. Thus, the policy analysis is completed twice in this case: once where a single F is found, per fishery, for the entire simulation period and once where there is one policy for the first twenty years and a second for the final twenty years of the simulation. The second policy does not begin until there has been an obvious change in productivity and system conditions.

"Optimal" policies implemented in nutrient models, with a change in nutrients

The two-stage policies (split policies) that are suggested as optimal by ECOSIM are implemented in IGBEM and BM2.

Nutrient scenarios vs the results of the optimisations with a change in nutrients

The change in nutrients has a much larger impact upon the system-level measures of catch and economic value than the results of the optimisations when there is a change in nutrients. Therefore, the outputs of these optimisations are compared to the scenarios where there is a change in nutrients, but no change in F.

Summary of conclusions for fishing policy results

A synthesis is made of the general results to come out of the fishing policy analysis and the many comparisons.

Table 7.5: Criteria used to define the objective functions used in the ECOSIM policy analysis routines.

(a) ecological weightings used in the ECOSIM analysis

	Strategies			
	Charismatic		All species represented	
Group	**Mandated Relative Biomass**	**Relative Weight**	**Mandated Relative Biomass**	**Relative Weight**
Phytoplankton	1	0	1	0
Small zooplankton	1	0	1.5	0
Large zooplankton	1	0	1.5	0
Deposit feeders	1	0	1.5	0.2
Scallops and mussels	1	0	5	0.4
Filter feeders	1	0	1	0.4
Inf. predators	1	0	1	0.2
Epi. predators	1	0	2	0.4
Sth rock lobster	1	0	5	1.4
Abalone	1	0	3	1.4
Other grazers	1	0	1.5	1.2
Scavengers	1	0	1	0.2
Microphytobenthos	1	0	1	0
Seagrass	1	1	1	0
Macroalgae	1	0	1	0
Clupeoids	1	0	2	0.8
Juvenile snapper	1	0	1	1.8
Snapper	4	0.1	4	2
Juvenile flatfish	1	0	1	1.2
Flatfish	1	0	2	2.4
Juvenile KG whiting	1	0	1	1.2
KG whiting	5	0.1	5	1.8
Juvenile piscivores	1	0	1	1.2
Piscivores	1	0	3	2.4
Juvenile mullet	1	0	1	2.4
Mullet and garfish	1	0	2	3
Other demersals	1	0	2	1.8
Southern calamari	1	0	2	0.6
Other cephalopods	1	0	1.5	0.8
Rays	1	0.1	1	4.2
Sharks	2	1	2	4.2
Birds	3	1	3	14.2
Marine mammals	4	1	4	11.2

(b) social weightings used in the ECOSIM analysis

Gear Type	Jobs/Catch
Purse seine	1
Scallop dredge	1
Haul seine	1
Longline	0.5
Mesh nets	1
Dive	0.2
Aquaculture	0.1
Pots	0.5

7.3 Results

7.3.A Comparison of the "base case" results

The final parameterisations of IGBEM and BM2 result in simulated systems that are fairly close to the summarised form of the bay as captured by the ECOPATH model.

Comparison of Biomasses

The majority of groups, both in IGBEM and BM2, have biomasses within a factor of two of the values for the balanced ECOPATH model (Table 7.6). However for IGBEM, this is a bare majority. Eight groups were more than a factor of two from the ECOPATH values. The benthic grazer and epifaunal predator groups are nearly three times larger than the corresponding group in ECOPATH, which may be symptomatic of IGBEM's apparent tendency to emphasise a trophic web based on primary production over the detritus-based web. The biomass of detritus is a factor of three lower for IGBEM.

Although it would be possible to tune IGBEM to more closely match more of the biomasses in PPB, this would entail moving a number of the clearance, growth and mortality parameters for the benthic groups beyond the biological limits currently recorded in the literature. This suggests that there may be an additional mechanism or property at work in the bay that IGBEM does not include or cannot capture. It may also suggest that the loss of epifauna to the 'static fish' (a constant loss term in IGBEM) may not be quite high enough (chapter 1). The macrophyte groups (seagrass and macroalgae) are much higher than the ECOPATH values and this is undoubtedly due to the spatial structure in IGBEM, which allows for a roughly five year cycle of "macrophyte-barrens" formation and recovery as nutrient availability interacts with the density of benthic grazers. A linked cycle of this form has not been recorded for PPB and this may be a model artefact. At the other extreme, the other benthic primary producer

Table 7.6: Comparison of the group data for the three models. The values are given as the relative size of the Biomass, P/B and Q/B values output by IGBEM and BM2 in relation to those in ECOPATH (value for model x / value in ECOPATH). The values are only given for those groups shared by all three models. To allow for this comparison, the plankton groups in the nutrient models are aggregated to the levels of ECOPATH; the benthic invertebrate groups in ECOPATH are aggregated to the level of trophic groups; the demersal fish of the nutrient models are equated with the flatfish in ECOPATH; and the herbivorous fish were equated with the mullets.

	IGBEM			BM2		
Group	**B**	**P/B**	**Q/B**	**B**	**P/B**	**Q/B**
Phytoplankton	1.09	1.42	-	1.21	1.12	-
Small zooplankton	1.37	0.70	0.69	1.40	0.68	0.67
Large zooplankton	1.14	1.03	1.02	0.77	1.09	1.24
Deposit feeders	0.80	2.12	0.80	1.20	1.89	0.59
Filter feeders	0.96	0.42	0.27	0.96	1.05	1.16
Infaunal predators	1.38	1.98	0.54	1.11	2.13	0.39
Epifaunal predators	2.92	1.13	0.55	0.64	1.08	0.57
Benthic grazers	2.49	0.27	0.08	0.85	2.34	0.70
Microphytobenthos	0.10	1.10	-	0.13	1.00	-
Seagrass	4.10	1.00	-	2.23	0.17	-
Macroalgae	2.01	0.25	-	1.01	0.74	-
Clupeoids	1.92	1.92	0.27	1.66	1.90	0.25
Juvenile flatfish	1.05	1.26	1.03	1.56	1.49	1.20
Flatfish	0.80	0.92	0.43	1.17	1.01	0.68
Juvenile piscivores	2.22	1.40	0.91	0.29	0.75	1.42
Piscivores	1.24	0.41	0.37	1.16	0.80	0.73
Juvenile mullet	0.64	3.50	1.15	0.92	2.90	1.05
Mullet	0.40	1.42	0.49	2.32	1.67	0.85
Detritus	0.30	-	-	1.34	-	-

(microphytobenthos) is only a tenth of the ECOPATH value. This is probably due to the competitive exclusion of the group by the large macrophyte groups and a poor calibration of a relatively new part of the final IGBEM model (chapter 1). This is an unfortunate consequence of the fact that the nutrient models were developed in another context prior to this particular investigation.

Within the fish groups, the biomass of juvenile piscivores in IGBEM is more than double that of the ECOPATH model, suggesting the survival of 0+ to 2+

individuals is probably too high in IGBEM. While the same groups prey on the juvenile piscivores in all three models, the mortality imposed by the static predators in IGBEM (sharks, birds and mammals) is tuned based on older age classes and total longevity of the fish group. As a result it does not seem to be high enough for the younger, more vulnerable, age classes. Further, as the elevated biomass is damped with the aging of cohorts into the older age classes, it is possible that the mortality rate of the oldest age classes is a little too high. Thus, while the mix of age-specific and general pressures on the fish groups serves to represent the dynamics of the intermediate age classes of the piscivorous fish group well, it does not perform as satisfactorily for the younger and older age classes. In contrast to the juvenile piscivores, the adult mullet biomass is two and half times lower in IGBEM than ECOPATH. This is due to additional mortality resulting from the starvation of mullet in IGBEM during those periods when the macrophytes are in a "barrens" state. Lastly, the biomass of the detritus in IGBEM was only a third of the estimate used in the ECOPATH model. This is a result of a combination of factors in IGBEM: the point source detrital input is about two thirds of what it should have been, the assimilation by the detritus feeders is too efficient and detrital burial is too fast.

The comparison of the biomass values in the BM2 and ECOPATH models shows that these two are much closer. Between the two, only the microphytobenthos, seagrass, juvenile piscivore and mullet groups differ by more than twofold. Microphytobenthos is once again only a tenth of that in the ECOPATH model, whereas seagrass is nearly three times higher in BM2 than in ECOPATH. These results suggest that more time should have been spent tuning the macrophytes and investigating whether or not it was possible to suppress their competitive exclusion of the microphytobenthos. The dynamics of the competitive exclusion and its relation to a "macrophyte-barrens" cycle, which is also displayed by BM2, are only obvious once the

full spatial models are considered (chapter 2) and will not be discussed here. It is worth noting that the "macrophyte-barrens" cycle in BM2 has a shorter period and is not of the same amplitude or as spatially widespread as that in IGBEM (chapter 2) and as a result has a smaller impact on the participating groups.

With regard to the fish, it is noteworthy that the same groups stand out in comparison to ECOPATH for both IGBEM and BM2, but that the direction of difference is reversed between the two nutrient models. Apparently the feeding and migration regimes in BM2 are different enough to allow for the dynamic predators to target the juvenile piscivores more effectively, while the adult mullet escape starvation.

Comparison of P/B and Q/B ratios

The comparison of P/B and Q/B ratios amongst the three models proves to be insightful. The P/B ratios produced by the nutrient models are generally close to those in the ECOPATH model, within a factor of two.

In IGBEM the P/B ratios for the benthic deposit feeders and juvenile mullet are more than twice as high as those in ECOPATH, while those for filter feeders, benthic grazers, macroalgae and piscivores are less than half. It may be that, with so many explicit processes to be parameterised in IGBEM, their cumulative effect can result in inappropriate levels of productivity. This would seem to be supported by the fact that all of the consumer groups with low P/B ratios also had low Q/B ratios. It is the low P/B ratio for macroalgae that cannot be easily explained.

For BM2, the P/B ratios for the infaunal predators, benthic grazers and juvenile mullet are all more than double those of ECOPATH, whereas the ratio for seagrass is less than half. The general form of the equations and the specific conversion efficiencies used for groups on diets of low nutritive value in BM2 may allow for P/Bs for consumers that are too high. Resetting the efficiencies of these groups to lower levels

could correct this problem. The mechanism causing the low levels of seagrass productivity is much harder to identify.

The Q/B ratios are much more easily explained. In general, the values produced by the nutrient models are often too low in comparison to those in ECOPATH . This suggests that overall the assimilative processes have the potential to be much more efficient in the nutrient models and may be too high, at least for some groups.

System-level indices

Another useful way to compare models is to use system or flow indices (Finn 1976, Ulanowicz 1986, Christensen 1995). A selection of such indices calculated for each of the models is given in Table 7.7. It is obvious that the models do not match as well under all the indices presented. Relative Ascendancy, Mean Trophic Level, Mean Trophic Level of the Catch, Primary Production / Biomass and Total Biomass / Total Throughput all suggest that the model systems are close in form and system maturity. In contrast, Finn's Mean Path Length, Net Primary Production and Total Biomass indicate

Table 7.7: A comparison of ten system-level indices for the "base case" runs of the three models. Finn's Recycling Index and Relative Ascendancy are given as proportions not percentages here. The bracketed figure for Mean Trophic Level of the Catch for ECOSIM and BM2 is the value when only finfish are considered as in IGBEM.

System index	ECOSIM	BM2	IGBEM
Finn's Mean Path length	4.0	4.9	3.6
Finn's Recycling Index	0.2	0.24	0.07
Mean Trophic Level	1.98	2.16	2.05
Mean Trophic Level Catch	2.8 (3.19)	2.42 (3.2)	3.28
Net Primary Productivity	3070.99	4860.84	4131.38
Primary Production/Biomass	14.12	13.56	13.74
Relative Ascendancy	0.32	0.30	0.33
System Omnivory Index	0.18	0.06	0.18
Total Biomass (excluding detritus)	217.45	358.0	300.69
Total Biomass / Total Throughput	0.016	0.015	0.023

large differences between the model systems. Finn's Recycling Index and the System Omnivory Index are intermediate, suggesting that one or other of the nutrient models is close to the ECOPATH model while the other is not. In combination these indices suggest that the gross form of the model systems are quite similar, while the internal details producing this form vary in some crucial respects.

Temporal Dynamics

Moving from the static to the dynamic, the patterns of biomass dynamics for the ECOSIM model are in good agreement with the temporal dynamics of the nutrient models, ignoring those dynamics caused by the spatial structure of the trophic models – such as the "macrophyte-barrens" cycles. Once forced by the time series of primary production, even the interannual variability in the ECOSIM model mirrors that of the nutrient models, especially for the dominant benthic deposit feeder group (Figure 7.4). Given that phytoplankton are commonly used as an indicator group in monitoring studies (via chlorophyll a measurements), it is worth noting that there is not a good match between the three models for the phytoplankton (Figure 7.5). This resulted from a lack of a seasonal and tidal cycle in the ECOSIM implementation, and a differential in the sensitivity to forcing in the nutrient models. The clupeoids (or planktivorous fish) are another group that show some notable differences in temporal pattern between ECOSIM and the nutrient models. This group is more responsive in ECOSIM than in the nutrient models (Figure 7.6). This is contrary to expectations based upon the dynamics of their prey species. Of the three models, the planktonic groups in ECOSIM show the least response to forcing. Thus, a reversal of responsiveness higher in the trophic web is not anticipated.

Figure 7.4: Overlay of a section of the time series of the benthic deposit feeder group in all three models. The period shown represents one cycle of the forcing function file. Light grey line is ECOSIM, dark grey line is BM2 and black is IGBEM.

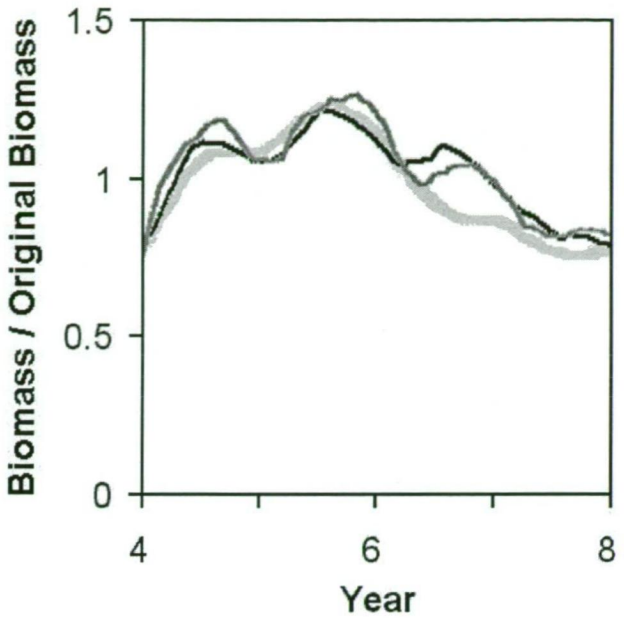


Figure 7.5: Overlay of a section of the time series of total phytoplankton for the three models. The period shown represents one cycle of the forcing function file. Light grey line is ECOSIM, dark grey line is BM2 and black is IGBEM.

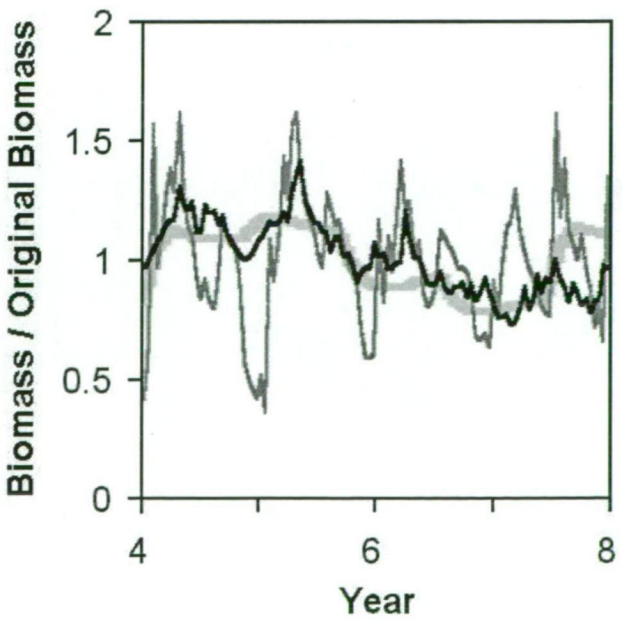
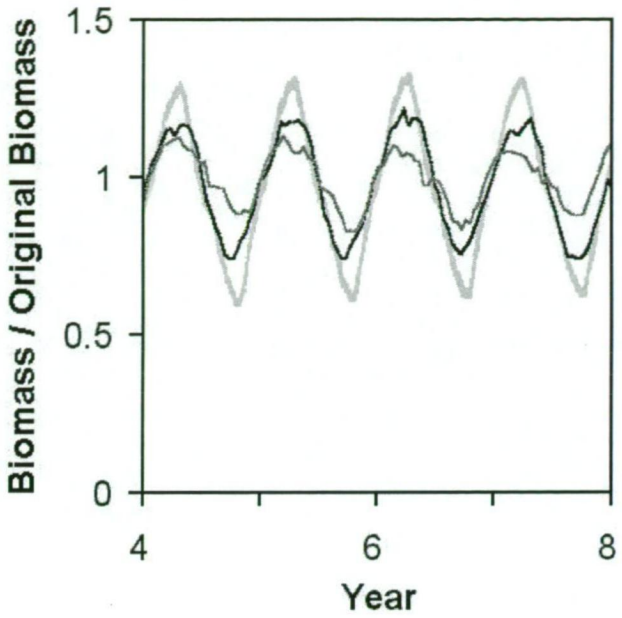


Figure 7.6: Overlay of a section of the time series of the planktivorous fish group (clupeoids) in all three models. The period shown represents one cycle of the forcing function file. Light grey line is ECOSIM, dark grey line is BM2 and black is IGBEM.



Alternative forcing scenarios

While there is relatively good agreement between models in the "base case" runs, greater differences between the models become apparent under changing conditions (fishing pressure or nutrient loading).

The period of transient dynamics in response to new ambient conditions is similar in all models. The most responsive (short lived, high turnover) groups reach their new densities within 2 years and the slower groups within 5 years. However some of the slower groups in ECOSIM appear to track their faster food groups too quickly, in comparison with the nutrient models.

The general patterns of biomass change seen in the three models under changing conditions are given in Table 7.8. On the whole, the qualitative changes seen in the groups as conditions changed do correspond – all the models agreeing (i.e. the direction of change matched) in 65% of cases. On an individual basis qualitative agreement is

even higher, ECOSIM agreed with BM2 in 72% of cases and with IGBEM in 78% of cases. In the majority of cases where the models do not agree, ECOSIM recorded no change whereas the nutrient models record some change. There is only direct disagreement (direction of change opposite) between ECOSIM and the nutrient models in less than 5% of cases. However, the magnitude of change often differs substantially between the various models. The magnitude of change observed in ECOSIM differs from that seen in BM2 by more than a factor of 2 in 27% of cases (in over half of those the magnitude of change differs by more than a factor of 5). In comparison, the magnitude of change seen in ECOSIM and IGBEM differs by more than a factor of 2 in only 19% of cases (less than half of which are cases where they differ by more than a factor 5). It is noteworthy that the cause of the divergences in the magnitude of change is not the same across all the scenarios. In those scenarios where it was the nutrient levels that change, it is usually the higher trophic groups of ECOSIM that show the most divergence, suggesting less buffering up the trophic web in ECOSIM than in the nutrient models. Conversely, in the scenarios where F changes with time it is the biomass of the groups (particularly the fish) within the nutrient models that undergo the greatest changes. The formulation of the consumption and closure terms in the various models is probably at least one of the explanations for these effects. The forage arena formulation in ECOSIM allows for compensatory dynamics, especially under stock declines. This is something the feeding formulations in the nutrient models do not capture nearly as well, if at all. Moreover, the dynamic top predator groups included in ECOSIM not only track their prey but are often bycatch groups themselves. As a consequence, when there are changes in F they undergo direct and indirect impacts on their population size and so react in a more complex fashion than the simple decline that the closure terms of the nutrient models allow. The end result is that the formulation of the food web interactions for the fish in the nutrient models cannot adjust for the effects

Table 7.8: The relative change in biomasses (biomass after change / biomass before change) for each of the three models under the test scenarios. As only qualitative comparisons are possible, the values presented are rounded in most cases. The lumping and association of groups noted for Table 7.6 also applies here. Due to their value as a potential indicator group, sharks are also given for ECOSIM.

(a) nutrient change scenarios

	Nutrient input rises			Nutrient input drops		
Group	**ECOSIM**	**BM2**	**IGBEM**	**ECOSIM**	**BM2**	**IGBEM**
Phytoplankton	6	2	10	0.15	0.5	0.2
Small zooplankton	6	2	5	0.15	0.5	0.1
Large zooplankton	10	1.2	4.5	0.1	0.75	0.15
Deposit feeders	2	2.2	3	0.5	0.1	0.3
Filter feeders	8	1.4	2	0.02	0.8	0.3
Infaunal predators	4	1.5	2	0.2	1	0.25
Epifaunal predators	8	1	4	0.2	1	0.3
Benthic grazers	0.5	0.8	0.3	1.3	2	1.5
Microphytobenthos	20	100	1.5	0.05	0.5	0.25
Seagrass	0.05	0.08	0.07	10	1.2	20
Macroalgae	4	5	0.1	0.05	0.75	1.2
Clupeoids	7	1.1	1.2	0.03	0.8	0.75
Flatfish	5	1	1	0.1	1	1
Piscivores	2	1.2	1.2	0.1	0.8	0.75
Mullet	0.05	0.75	0.75	4	1	0.75
Sharks	9	-	-	0.25	-	-
Detritus	2	2	2.5	0.3	0.8	0.5

(b) change in F scenarios

	Fishing pressure rises			Fishing pressure drops		
Group	**ECOSIM**	**BM2**	**IGBEM**	**ECOSIM**	**BM2**	**IGBEM**
Phytoplankton	1	1.1	1	1	0.1	1
Small zooplankton	0.75	0.05	1.2	1.2	2	1.2
Large zooplankton	1.5	2	1.5	0.75	0.01	0.75
Deposit feeders	1	1	1	1	1	1
Filter feeders	0.5	0.001	0.8	1.2	1.1	1.1
Infaunal predators	1	1	1	1	1	1
Epifaunal predators	1.2	0.005	1.2	0.9	1	0.9
Benthic grazers	0.75	0.001	0.75	1.2	4	1.2
Microphytobenthos	1	1	1	1	0.5	1
Seagrass	1.2	1.2	1.2	0.9	0.9	1
Macroalgae	1	1	1	1	1.5	1
Clupeoids	0.3	0.1	0.2	1.5	2	1.5
Flatfish	0.5	0.05	0.12	1.2	2.5	2
Piscivores	0.8	0.2	0.15	1.1	2.5	2
Mullet	0.12	0.1	0.3	1.5	2	1.5
Sharks	0.25	-	-	1.5	-	-
Detritus	1	0.4	1	1	1	1

of top-down fishing-imposed pressures as effectively as the formulation implemented in ECOSIM.

Beyond these general observations, one of the most notable points is that microphytobenthos increases by two orders of magnitude in BM2 under rising nutrients, while macroalgae declines to negligible levels in IGBEM. Both of these responses can be traced back to the size of the phytoplankton blooms produced by each model as nutrient input rises. IGBEM produces quite intense blooms, which starve the underlying macrophytes of light and so even the macroalgae cannot compete. This is not the case in BM2 where only moderate blooms occur. In this case enough light reaches the sediment, but epibenthic fouling kills off the seagrass allowing microphytobenthos to take its place and spread from that foothold. Both of these patterns have been identified in eutrophied systems (Conley 1999, Herbert 1999, Lotze et al. 1999), though the pattern produced by IGBEM is more common.

Consideration of the system indices (Table 7.9) in conjunction with the patterns of biomass change again shows that consideration of multiple indicators is necessary for the formation of a complete picture. Between them, the Mean Trophic Level indices and the Total Biomass do capture the fact that the model systems shift in much the same way, just to different extents. However, they don't reflect the changes in the levels of biomass that occur in some groups.

Across all the measures used to compare the models, it is noteworthy that there is no consistent grouping of the models. Given their similar origins and internal premises one might expect that IGBEM and BM2 would behave in a similar way. This is true for the groups in the nutrient models that are modelled in a similar fashion, such as the fish groups. It is not the case for many of the other groups where the formulations are quite different between IGBEM and BM2 (the differences noted in Table 7.1 are strongest in the non-fish groups). For instance the water column groups in BM2 do not

Table 7.9: System-level indices for all the simulations. The bracketed figure for Mean Trophic Level Catch for ECOSIM and BM2 is the value when only finfish are considered as in IGBEM.

STATUS QUO SIMULATION			
System Index	**ECOSIM**	**BM2**	**IGBEM**
Mean Trophic Level	1.98	2.16	2.05
Mean Trophic Level Catch	2.8 (3.19)	2.41 (3.2)	3.28
Total Biomass	217.45	359.0	300.69

BASE CASE SCENARIOS

	Nutrient input rises			**Nutrient input drops**		
System Index	**ECOSIM**	**BM2**	**IGBEM**	**ECOSIM**	**BM2**	**IGBEM**
Mean Trophic Level	2.09	2.21	2.37	2.0	2.22	1.8
Mean Trophic Level Catch	2.73 (3.21)	2.74 (3.08)	3.27	1.97 (2.26)	2.84 (3.09)	3.32
Total Biomass	1731.65	629.57	646.22	23.13	159.83	196.21
	Fishing pressure rises			**Fishing pressure drops**		
System Index	**ECOSIM**	**BM2**	**IGBEM**	**ECOSIM**	**BM2**	**IGBEM**
Mean Trophic Level	1.99	2.26	2.01	2.01	1.98	2.15
Mean Trophic Level Catch	2.98 (3.23)	2.76 (3.12)	3.37	2.68 (3.2)	2.91 (3.04)	3.26
Total Biomass	218.48	331.95	289.48	220.21	245.40	314.65

FISHERIES POLICY RUNS

	Economic Strategy			**Ecological Strategy**		
System Index	**ECOSIM**	**BM2**	**IGBEM**	**ECOSIM**	**BM2**	**IGBEM**
Mean Trophic Level	1.97	2.1	2.28	2.01	2.24	2.49
Mean Trophic Level Catch	2.87 (3.2)	2.86 (3.42)	3.48	2.72 (3.21)	2.29 (3.04)	3.64
Total Biomass	215.3	134.62	259.86	220.42	381.72	316.25
	Nutrients Rise					
	Split Economic			**Split Ecological**		
System Index	**ECOSIM**	**BM2**	**IGBEM**	**ECOSIM**	**BM2**	**IGBEM**
Mean Trophic Level	2.00 – 1.95	2.24 – 2.22	2.41 – 2.46	2.00 – 2.03	2.20 – 2.23	2.38 - 2.44
Mean Trophic Level Catch	2.76 – 2.6 (3.20 - 3.20)	2.82 – 2.89 (3.06 - 3.08)	3.52 – 3.55	2.80 – 2.69 (3.21 - 3.20)	2.84 – 2.91 (3.04 - 3.09)	3.46 - 3.54
Total Biomass	217.44 – 1401.16	387.44 – 805.4	393.84 – 396.47	217.31 – 1366.65	316.89 – 833.56	383.05 – 388.64
	Nutrients drop					
	Split Economic			**Split Ecological**		
System Index	**ECOSIM**	**BM2**	**IGBEM**	**ECOSIM**	**BM2**	**IGBEM**
Mean Trophic Level	1.98 – 2.04	2.2 – 2.31	2.39 – 2.41	2.01 - 2.06	2.21 – 2.28	2.61 – 2.43
Mean Trophic Level Catch	2.88 – 2.02 (3.16 - 2.20)	2.84 – 2.90 (3.04 - 3.09)	3.51 – 3.52	2.86 - 1.93 (3.21 - 2.74)	2.52 – 2.13 (3.03 - 3.05)	3.66 – 3.56
Total Biomass	216.68 – 39.5	316.1 – 271.29	258.01 – 232.93	220.18 – 39.98	349.42 – 308.6	301.59 – 226.64

react as strongly as those in IGBEM, which respond similarly to those in ECOSIM (despite the omission of light and nutrient limitation from the ECOSIM formulation).

Summary of conclusions for "base case" results

The history of each model's development is quite telling and the nutrient models may have benefited from more tuning. In spite of this a number of general conclusions can be drawn. The ECOSIM model is not as buffered against nutrient related changes as the nutrient models are, but it is more buffered against changes in the fisheries. The spatial structure of the nutrient models also allow for the expression of some more complex model behaviour. In general the behaviour of the low to middle trophic groups in the nutrient models is probably more realistic than that in ECOSIM, but the higher trophic groups react more sensibly in ECOSIM than the nutrient models. This is probably another consequence of their respective focus and development histories.

7.3.B Fishing policy analysis

The open and closed loop policy optimisation features of the ECOSIM software are used to explore "optimal" fishing strategies (Fs for each fishery) given a range of economically and ecologically weighted objective functions.

The main strategies suggested by the policy analysis are then implemented in the nutrient models to see if the outcomes agreed with those predicted by ECOSIM. For ease of understanding, the ECOSIM optimisations will be presented and then the outcomes of the nutrient models will be discussed. This two step presentation will then be repeated for the optimisation done when nutrient forcing changes during the period of the simulation. As with the comparisons discussed above, there is usually qualitative agreement between the models, though specific responses can vary widely.

ECOSIM, with no change in nutrients

The results of the ECOSIM policy analyses under constant environmental conditions are summarised in Table 7.10. A full description is given below, but in short, over the entire range of objective function weightings trialed, only three results are produced: an economically based strategy, an ecologically based strategy, and a compromise between the two. These outcomes also persisted, with very little change, across a range of refuge parameter settings used in a sensitivity analysis performed on the model and optimisation process.

Table 7.10: Results of the policy analyses under constant environmental conditions. The Fs given are those found by the ECOSIM open loop analysis (with a *Status Quo* entry included for comparative value) and the summary statistics are for the ECOSIM output under the suggested Fs. The Overall Average Total Catch and Total Value indicate the cumulative totals over the entire run. The "Ratio End/Start Values" are the ratios of the instantaneous total catch, economic value and biomass at the beginning and end of the run.

	Strategy				
	Status Quo	**Economic**	**Ecological (no mand.)**	**Ecological (mand)**	**Compromise**
Weighting					
Economic	-	1	0.0001	0.0001	0.5
Social	-	0.0001	0.0001	0.0001	0.5
Mandated rebuilding	-	0.0	0.0	10	1
Ecosystem	-	0.0001	1	1	1
Estimated Relative Fs					
Purse seine	1	1.9	0.9	0.4	1.7
Scallop dredge	1	2.0	0.2	0.2	3.0
Haul seine	1	0.5	0.005	0.02	0.2
Longline	1	1.2	0.04	0.06	0.5
Mesh nets	1	20.1	0.3	0.2	1.1
Dive	1	1.3	2.6	0.4	1.2
Pots	1	0.75	0.5	0.2	0.6
Aquaculture (omitted from search)	1	1	1	1	1
Overall Average					
Total Catch (t/km^2)	880	1420	570	376	1161
Total Value ($x10^6$)	1.2	1.9	0.7	0.5	1.4
Ratio End/Start Values					
Total Catch	1	0.56	0.97	1.15	0.76
Total Value	1	0.77	0.4	1.46	0.89
Total Biomass	1	0.79	1.05	1.1	0.91

The "economic" strategy sees the Fs increase, relative to current levels, for all but the haul seine and pot fisheries. The mesh net fishery undergoes the most extreme change as the optimisation suggests increasing its F to 20x current levels (Table 7.10). The resulting biomasses (Figure 7.7) indicate that under the proposed set of Fs, the sharks and flatfish are effectively extirpated. By reducing these predatory groups, their higher value prey species can flourish, thus improving the economic performance to about 1.5x *status quo* levels. Among the invertebrate fisheries, the increase in F produces a moderate decline in the biomass of the high value species, abalone and scallops. Within the bycatch species the most important effects are that, under this economically optimal set of Fs, the big piscivorous finfish and the marine mammals decline to about half of their *status quo* levels. The drop in these groups furthers the release from predation of the high value prey species (King George whiting and southern rock lobster, see Figure 7.7), the mechanism apparently motivating the very large increase in F for the meshnet fishery. In spite of the overall increase in total catch and value relative to *status quo*, the widespread depletion of so many groups causes the annual catch and value to drop by nearly a quarter and biomass by almost half from the beginning to the end of the simulation.

The "economic" strategy shows the least sensitivity to changes in the refuge parameters, though the species currently considered most heavily impacted by fishing (snapper, King George whiting and southern rock lobster) do vary a little from case to case. Overall, the only significant change is when all v's are set to 0.7, which sees a flip to a result more closely resembling the standard "ecological" strategy described below.

A variety of weightings of the ecological objective function all produce largely similar results (Figure 7.8), with lower Fs for the majority, if not all, the fisheries (Table 7.10). The one fishery that is sensitive to the ecological objective function and criteria chosen is the dive fishery for abalone. When mandatory population restoration is given

Figure 7.7: Plot of ECOSIM biomass trajectories under the Fs that result from an economically oriented objective function. Note that, in the interests of plot clarity, interannual variation in forcing has been removed here.

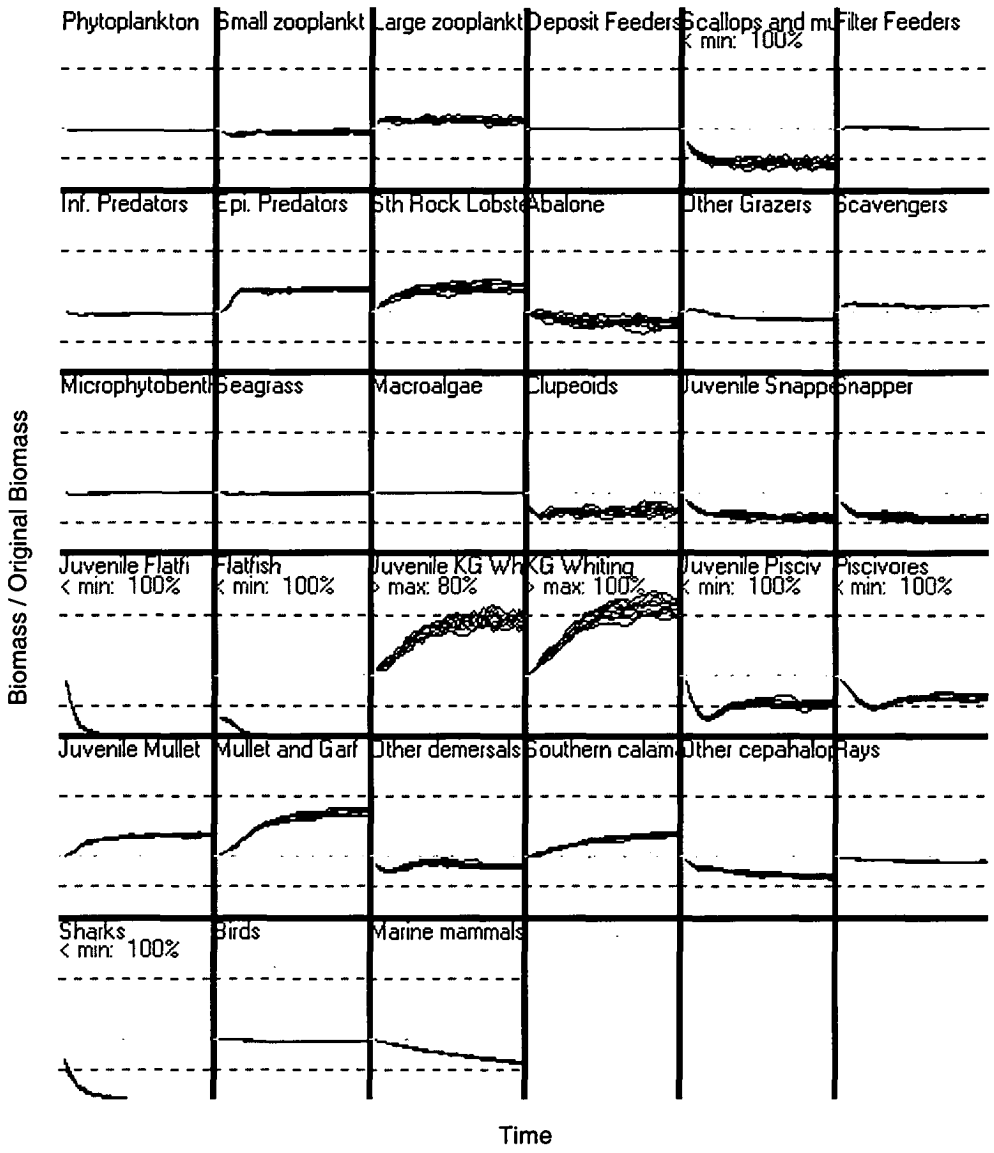
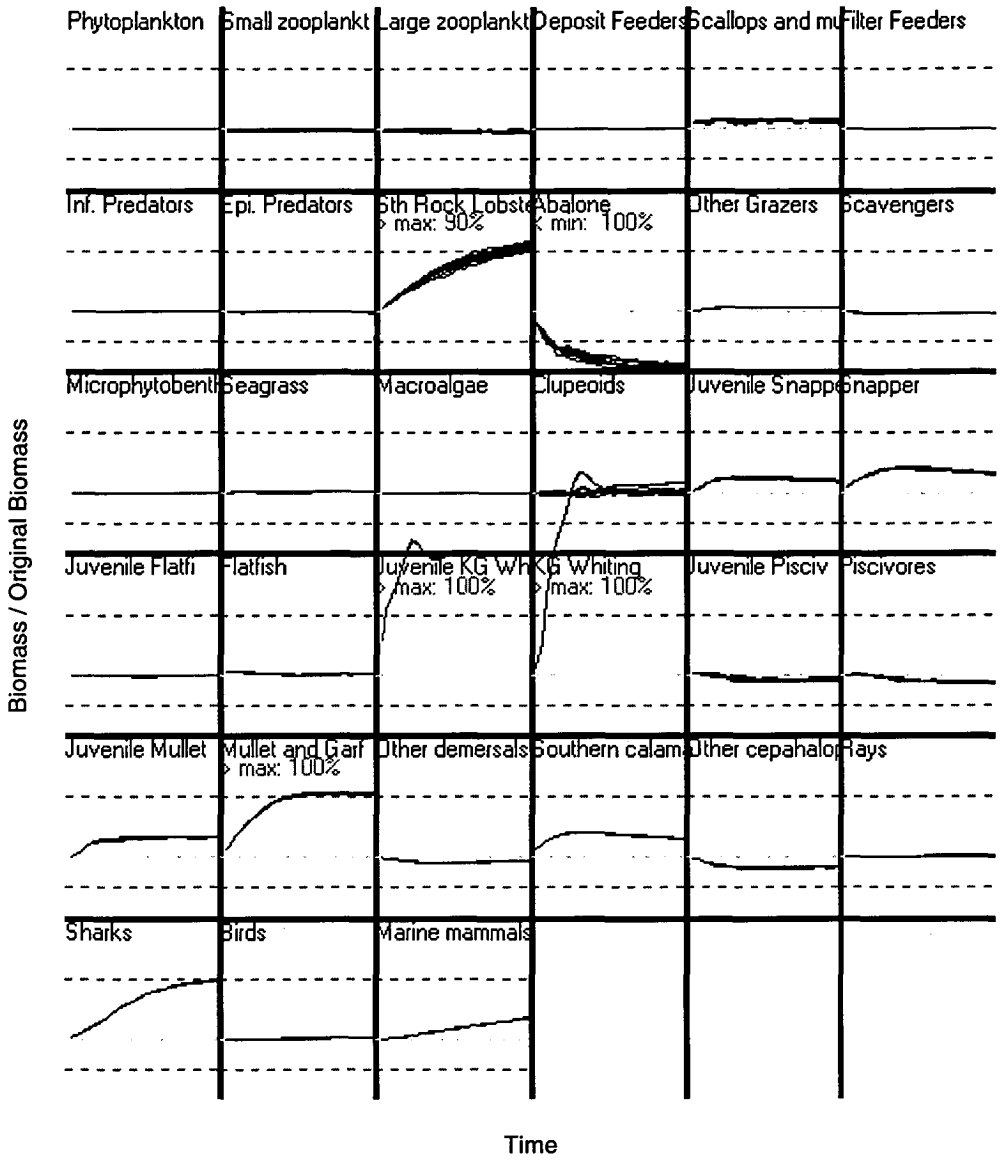
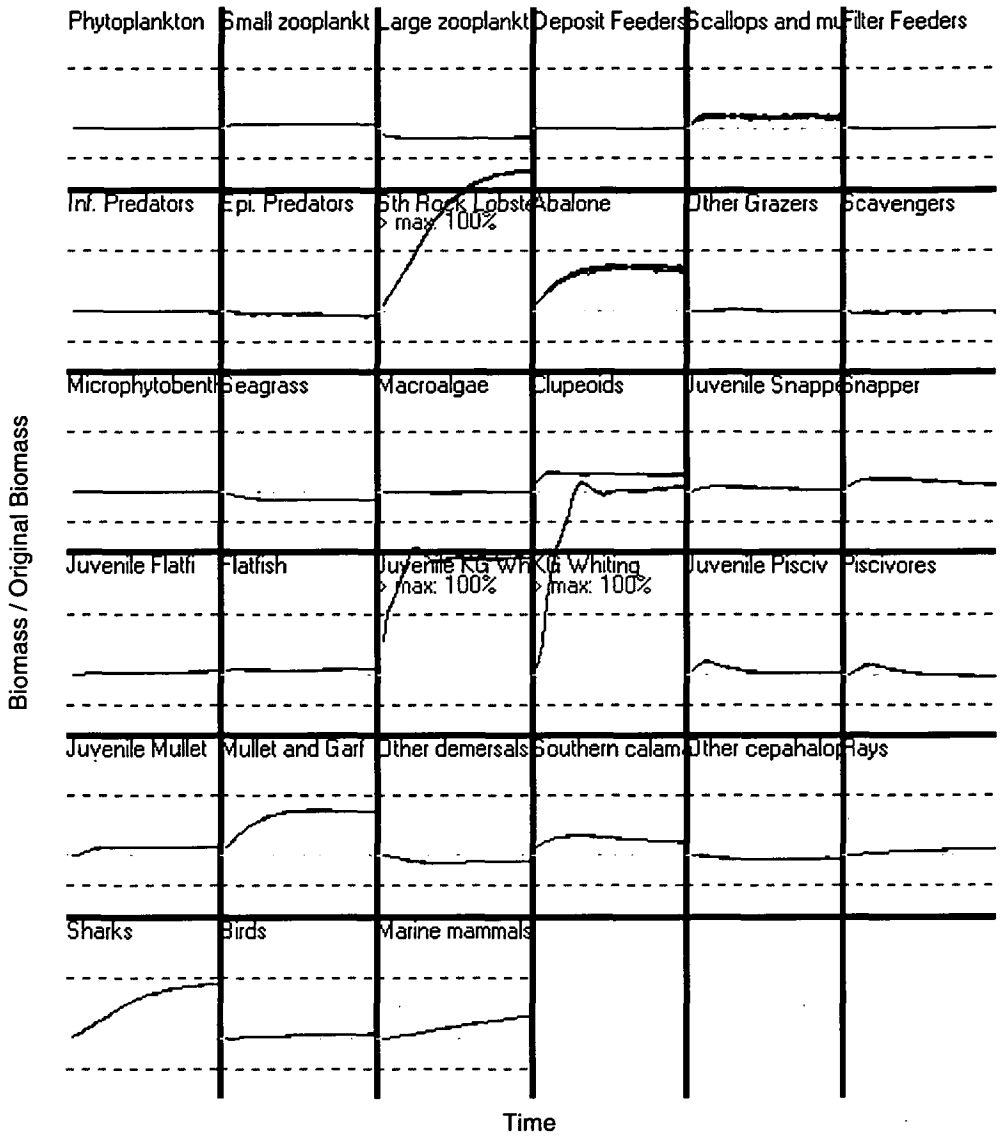


Figure 7.8: Plot of ECOSIM biomass trajectories under the Fs that result from an ecologically oriented objective function.

(a) with no mandatory stock restoration implemented,



(b) with some mandatory stock restoration implemented and ecological weighting given to all species not just those of immediate social interest. Note that, in the interests of plot clarity, interannual variation in forcing has been removed here.



little or no weight, the F for abalone fishery actually increases. This is probably due to its competition with the mullets (a fish identified as a group to be conserved or restored) and its very high market price (which is still of some importance given the small but non-negligible economic weight in the objective function). This results in the abalone biomass being depressed to the level of commercial extinction (Figure 7.8a) and the annual total value, for that run, falling by more than half. In contrast, when mandatory population restoration and maintenance are given at least some weight, the F for the dive fishery either remains at current levels or falls with the other fisheries. This indicated how critical the ecological criteria can be to certain species. If ecological concern is focused only on the charismatic or favoured recreational species then other components of the ecosystem, such as the abalone, continued to be quite intensively exploited (Figure 7.8a). When ecological criteria emphasise at least some conservation of all groups a much more balanced, mature system results (Figure 7.8b). However, this balance comes at the expense of the landed catch, with the total catch falling to about a quarter of that taken under the economic objective, while the total value is down by more than two thirds. The low Fs do allow the target groups to grow steadily though and the annual catch, value and biomass all rise from the beginning to the end of the period. Even with a low exploitation rate, the value of the pot fishery more than doubles, increasing the average total value of all fisheries.

The "ecological" strategy is more heavily impacted by changes in the refuge parameters, with the greatest variation in behaviour shown in the high value epifaunal groups, as well as in the cephalopods and the snapper groups. Nevertheless, there is little qualitative change in the predictions. The most significant variations are observed at low refuge parameter settings (v=0.2), where a more "even" ecosystem (one not so heavily skewed toward the charismatic species) results regardless of the explicit ecological criteria specified.

Attempts to find a compromise between the ecologically and economically based optimisations do not identify a smooth transition from one to the other. Rather, as the weightings are gradually changed from economically to ecologically dominated, the "economic" strategy given above persists as the optimal outcome for a wide range of weightings. It is not displaced as the optimal policy outcome until the point where the economic:ecological weight equalled 0.71:1. At this point there is a flip-point, which sees the optimal outcome returned as either the "economic" or "compromise" strategy depending on the initial start point of the search routine. The "compromise" strategy (Figure 7.9 and Table 7.10) closely resembles the "economic" strategy and is apparently heavily influenced by the economic contribution to the objective function. This is obvious not only from the pattern of biomass change, but also from a majority of the F settings, the total catch and value of the entire run and the instantaneous catch, value and biomass results. A direct comparison of the important statistics for the three main optimisation solutions can be found in Table 7.11. Many of the values for the "compromise" strategy are very similar to those for the "economic" strategy. However, the ecosystem contribution is still present and showed up in the values of the predatory species, which are depressed under the "economic" strategy. These groups do not suffer the excessive depletion under the compromise strategy. The biomass of the snapper groups reverses the pattern of change seen under the "economic" strategy and increases rather than decreases; while that of the sharks and marine mammals remain at *status quo* levels and the flatfish are not depleted to the point of extinction. As the objective function weightings are moved still further, this "compromise" strategy is the only outcome returned until the point where the economic:ecological weight equalled 0.5:1. From this point on, as the economic weighting is reduced still further, the optimal strategy is the "ecological" strategy.

Figure 7.9: Plot of ECOSIM biomass trajectories under the Fs that result from an objective function that is weighted for a compromise of the ecological and economic strategies. Note that, in the interests of plot clarity, interannual variation in forcing has been removed here.

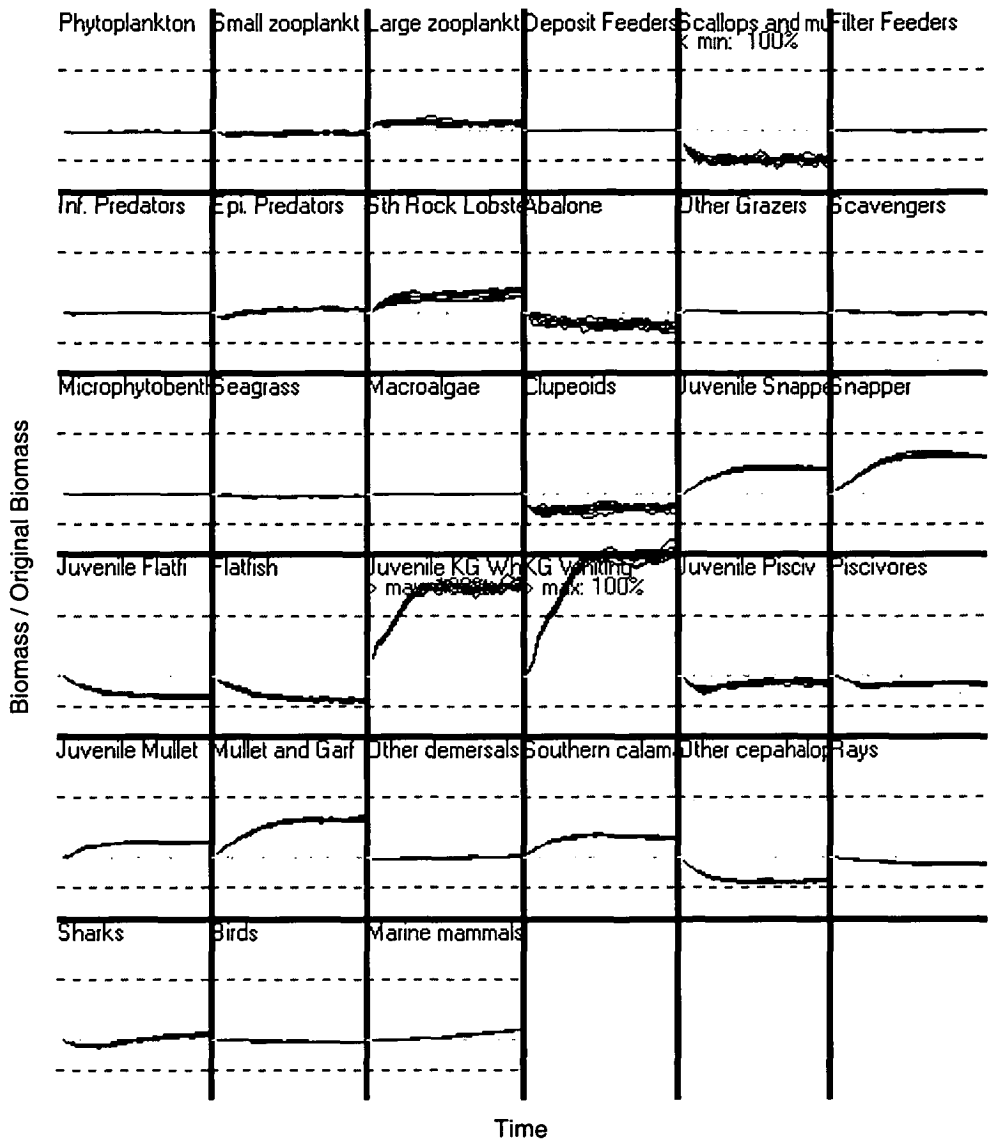


Table 7.11: Comparison of the important "economic", "ecological" and "compromise" strategies. The "ecological" strategy refers to the case where there is mandatory restoration of groups. The relative change in biomass indicates the ratio of the biomass that results from the implementation of the fisheries policy: the *status quo* biomass for the group. Only groups that demonstrate significantly different biomass trajectories between the various strategies are given. For flatfish and snapper the juvenile and adult groups act in the same way, so only the values for the adult group are provided.

	Strategy		
	Economic	**Compromise**	**Ecological**
Estimated Relative Fs			
Purse seine	1.9	1.7	0.4
Scallop dredge	2.0	3.0	0.2
Haul seine	0.5	0.2	0.02
Longline	1.2	0.5	0.06
Mesh nets	20.1	1.1	0.2
Dive	1.3	1.2	0.4
Pots	0.75	0.6	0.2
Relative change in biomass			
Large zooplankton	1.1	1.1	0.9
Scallops and mussels	0.7	0.7	1.2
Epifaunal predators	1.4	1.0	0.9
Southern rock lobster	1.35	1.4	3.0
Abalone	0.8	0.9	1.5
Seagrass	0.95	0.95	0.9
Clupeoids	0.9	0.9	1.1
Snapper	0.9	1.4	1.2
Flatfish	<0.01	0.8	1.1
Other cephalopods	0.75	0.6	0.9
Rays	0.95	0.9	1.1
Sharks	<0.01	1.5	1.9
Mammals	0.75	1.2	1.4

Table 7.12: The relative change in biomasses (biomass under new policy / "base case" biomass) for each of the three models under the ecological and economically based strategies. The lumping and association of groups noted for Table 7.6 also apply here and sharks are given for ECOSIM.

	Economic Strategy			Ecological Strategy		
Group	**ECOSIM**	**BM2**	**IGBEM**	**ECOSIM**	**BM2**	**IGBEM**
Phytoplankton	1	2	2	1	1	1.5
Small zooplankton	1	1	3	1	0.9	4
Large zooplankton	1	4	1.2	1	1.2	0.9
Deposit feeders	1	5	2	1	0.75	0.75
Filter feeders	0.5	0.01	1.5	1.2	1.2	2
Infaunal predators	1	1	1.5	1	1	1.5
Epifaunal predators	1.5	0.1	1.5	1.7	3	1.5
Benthic grazers	0.9	2	0.5	1.5	1.5	0.3
Microphytobenthos	1	2	1	1	1	1
Seagrass	1	1	1	0.75	1.1	20
Macroalgae	1	1	2	1	1	3
Clupeoids	0.8	0.5	0.5	1	1	1
Flatfish	0.1	0.01	0.02	1.5	3	1.5
Piscivores	0.5	0.75	0.75	0.75	5	2
Mullet	1.5	2	1.2	2	2.5	2
Sharks	0.05	-	-	2	-	-
Detritus	1	0.5	2	1	1.5	1.5

"Optimal" policies implemented in nutrient models, with no change in nutrients

The sets of Fs associated with the two strategies ("ecological" and "economic") identified by the ECOSIM policy optimisation routines are tested in IGBEM and BM2. The relative changes in biomass for all three models are given in Table 7.12.

Under the ecologically oriented set of Fs there is very good qualitative agreement between the three models with regard to the biomass trajectories of the various groups. There are some minor differences between IGBEM and the other two models, due to the fact that IGBEM does not allow for the fishing of invertebrates. Attempts to mimic fishing mortality in these groups using general background (natural) mortality did not succeed. The majority of the differences seen between IGBEM and the other two models, in this case, are due to this failure and its cascade effects. The more

important divergence between the ECOSIM and nutrient model predictions is in the piscivorous groups. The nutrient models predicted that the piscivorous fish would increase, whereas ECOSIM suggests that the group would decline marginally. This difference is almost certainly due to the fact that the highest trophic levels (sharks, birds and marine mammals) are only static not dynamic components of IGBEM and BM2. In ECOSIM these groups are free to change with the system, and impact the piscivorous group accordingly.

When the economically driven set of Fs are applied in IGBEM and BM2, there is, again, wide qualitative agreement between the time-series produced by the models. In this case all the models are in agreement over the impact of the proposed fishing mortalities on the fish groups. The same does not hold true for the invertebrate groups. As with the ecological case, IGBEM predicts an increase in the filter feeders, while the other models do not. BM2 actually predicts a collapse in the population of filter feeders, leading to a significant drop in the epifaunal predators (despite the drop in F for the pot fishery). This in turn releases the benthic grazers and allows that biomass to grow (despite the increase in F for the dive fishery). Thus, due to food web interactions, two of the three harvested invertebrate groups respond contrary to what would be expected from a simple consideration of the change in F of the fisheries targeting them.

Another important difference between the models is in the detritus, where there is no concurrence between any of the models – ECOSIM predicts no change, BM2 a twofold drop and IGBEM a twofold increase. This appears to be due to the dynamics of the major detritus producers and consumers in each model. The collapse of the flatfish and epifaunal predators in BM2 allows the deposit feeders in that model to increase by fivefold and this in turn depletes the standing stock of available detritus. In IGBEM the major producers of detritus (the primary producer groups) all increase, leading to an increase in the amount of detritus. The biomass of deposit feeders in IGBEM does

increase a little, but not to the extent seen in BM2 as the epifaunal carnivores also increase and kept the deposit feeders in check. Consequently, the detritus remains slightly higher than the *status quo* level. In ECOSIM there is no change in the biomass of the major producers or consumers of biomass so the detritus remains unchanged.

The system indices (Table 7.9) do capture the general shifts in the model systems and the fact that the shift differs between the models. The much larger response by the harvested groups in the nutrient models is reflected in the much greater changes in Total Biomass, relative to the *status quo* value (Table 7.9), displayed by these models. Further, the three indices taken as a whole also highlight the fact that overall ECOSIM does not respond as strongly over as many groups as the nutrient models do. However, these system-level indices do not capture the very large responses in a few of the groups.

Change in F scenarios vs the results of the optimisations

At face value, the "economic" strategy could be equated with the scenario where there is a general increase in F (Table 7.8b). Similarly, the "ecological" strategy could be equated to the scenario where there is a general decrease in F (Table 7.8b). Comparing these results, a few very important differences can be observed between the patterns of change in the two cases.

For ECOSIM, the most notable contrast is that a general (across the board) rise in F results in a decline in the mullet, whereas this group increases under the "economic" strategy. Several differences are apparent for the nutrient models. In IGBEM, the response of two groups differs in comparing the "ecological" strategy with the general decrease in F. The benthic grazers fall under the "ecological" strategy (Table 7.11), while they do not change at all under the general decrease in F (Table 7.8b). In turn this contributes to a sizeable increase in the biomass of seagrass. Comparing results

from the four strategies for BM2, many more groups show very different responses in biomass. Comparing the "ecological" strategy with the "drop in F", the greatest contrast occurs with the phytoplankton and large zooplankton. They remain relatively steady under the "ecological" strategy, but both groups decline severely in the scenario where there is a general decrease in F. Comparing the "economic" strategy with the "rise in F", a number of groups show different responses. The small zooplankton, deposit feeders, benthic grazers, epifaunal predators and mullet are all much higher under the "economic" strategy than under the general increase in F.

These differences appear to be due to at least two proximate factors. First, the changes in F under the optimal policies are not all of the same size (as is the case under the blanket change in the scenarios) and some fall or rise by much more (or less) than fivefold. Secondly, under the "economic" strategy the Fs do not increase for all groups (the Fs for the Haul seine and Pot fisheries actually fall). Both these factors can clearly lead to differences in biomass response between the fished groups. However the differences in the non-fished groups are not directly attributable to changes in F. Several groups that are predators, prey or competitors of the harvested groups show very different responses between the scenarios of broad changes in F and the specific sets of F suggested by the optimisations. This is something single species models would obviously not be able to predict.

Fishing policy analysis by ECOSIM, with a change in nutrients

A summary of the outcomes of the ECOSIM policy analyses under changing nutrients and ecological or economic criteria is given in Table 7.13.

For an economically oriented objective function, there is little difference in Fs between the cases of constant and decreasing nutrients. In contrast, Fs under

Table 7.13: Results of the policy analyses under changing environmental conditions. The Fs given are those found by the ECOSIM open loop analysis and the summary statistics are for the ECOSIM output under the suggested Fs. The Overall Average Total Catch and Total Value indicate the cumulative totals over the entire run. The "Ratio End/Start Values" are the ratios of the instantaneous total catch, economic value and biomass at the beginning and end of the run.

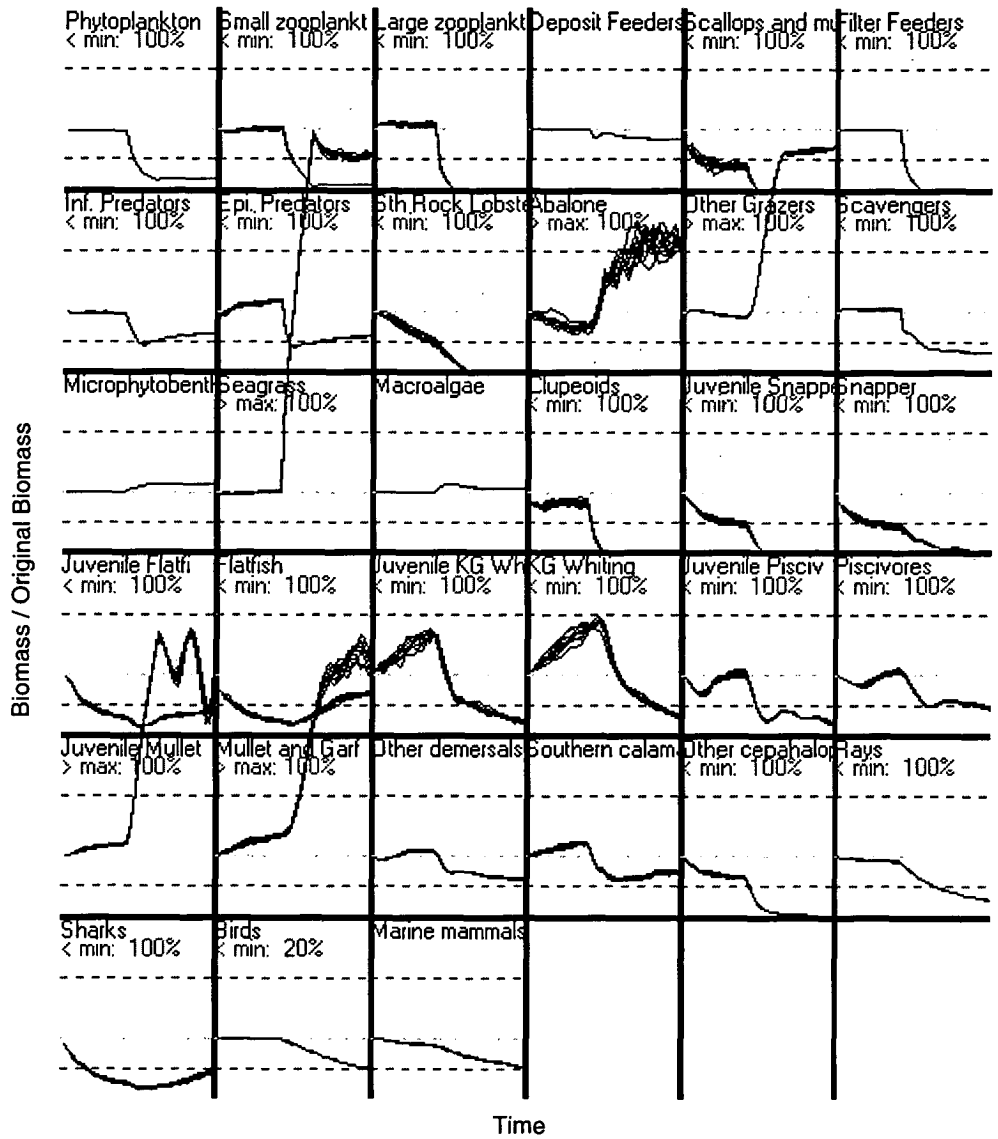
	Nutrients Rise				Nutrients drop			
	Single Economic	**Split Economic**	**Single Ecological**	**Split Ecological**	**Single Economic**	**Split Economic**	**Single Ecological**	**Split Ecological**
Estimated Relative Fs								
Purse seine	1.3	1.1 – 1.15	0.7	1.6 – 1.1	1.8	1.75 – 1.3	0.4	0.1 – 1.1
Scallop dredge	2.1	0.8 – 1.5	1.5	1 – 1.2	2.45	2 – 0.5	0.2	0.08 – 0.3
Haul seine	1.25	0.8 – 1.1	0.5	0.6 – 1	0.6	0.5 - 1	0.02	0.02 – 0.02
Longline	0.85	1.2 – 1.3	0.9	0.6 – 1.1	1.9	2.5 – 0.75	0.06	0.03 – 0.06
Mesh nets	0.65	1.4 – 1.1	1.1	0.7 – 1.9	15.0	11.9 – 0.7	0.1	0.01 – 0.3
Dive	0.9	1.2 – 0.7	1.3	0.5 – 1.2	1.9	1.2 – 2.4	0.45	0.25 – 0.6
Pots	1.5	1.1 – 2.1	0.9	1.7 – 1.4	1.1	0.9 – 1.2	0.1	0.1 – 0.1
Aquaculture (omitted from the search)	1	1 - 1	1	1 - 1	1	1 - 1	1	1 - 1
Overall Average								
Total Catch (t/km^2)	5267	4325	4030	4028	931	813	221	169
Total Value (x10^6)	5.6	5.5	5.0	5.1	1.4	1.2	0.5	0.4
Ratio End/Start Values								
Total Catch	6.59	6.86	6.6	4.77	0.02	0.06	0.01	0.04
Total Value	6.15	6.03	5.77	4.56	<0.01	<0.01	<0.01	<0.01
Total Biomass	2.35	2.3	2.29	2.28	0.72	0.73	0.73	0.73

increasing nutrients diverge from those found to be optimal with no change in nutrients for all but the scallop dredge and purse seine fisheries. The optimal policy in this case is more a mix of the "economic" and "ecological" strategies when there is no change in nutrients. The Fs for the purse seine, longline and dive fisheries are basically averages of the "economic" and "ecological" strategies for those fisheries. The Fs for the scallop dredge, haul seine and pot fisheries are the same size as, or even larger than, those for the "economic" strategy baseline, while the meshnet fishery is almost as low as in the "ecological" strategy when there is no change in nutrients.

With an economically oriented objective function, the set of two policies (split-policies) chosen under a fall in productivity was intuitively reasonable. The policy begins by following the path of the "economic" strategy suggested when there is no change in nutrients. Once the change in productivity occurs the split policy changes from one resembling the "economic" strategy to the "ecological" one as the policy optimisation attempts to correct for the declines initiated by the drop in productivity (Figure 7.10). For rising nutrient inputs the response is somewhat different. Depending on the basal food group (phytoplankton or detritus vs macrophyte), some sub-webs increase substantially while others collapse. As a consequence, the objective function surface seems to have become highly complex and the best result that can be found is to stay fairly close to current Fs both before and after the change in conditions.

Under an ecological objective, the solutions produced under constant conditions and the single solution when productivity falls are substantially similar. However, in this case the Fs suggested for the meshnet and pot fisheries are about half of those under constant conditions – as would be expected given the reduction in the target groups of these fisheries with the fall in productivity. As with the economic objective, the single F spanning a rise in productivity is different from that for the constant conditions. The result is much closer to the "economic" than the "ecological" strategy obtained when

Figure 7.10: Plot of ECOSIM biomass trajectories under the split Fs that result from an economically oriented objective function applied when there is a drop in productivity. Note that, in the interests of plot clarity, interannual variation in forcing has been removed here.



there is no change in nutrients. All but the purse seine and meshnet fisheries have Fs at or just below the level of those for the constant "economic" strategy. For the two exceptions (purse seine and meshnet) there are substantial increases in F in comparison with constant conditions (rising by two and six-fold respectively). Despite this, these two fisheries are still closer to the standard "ecological" strategy.

When a split policy is implemented with an ecologically weighted objective

function, results under both increasing and decreasing productivity appear to be intuitively reasonable, though some of the details are surprising. In the case where productivity rises over time, the solution is as expected. It begins by paralleling the constant "ecological" strategy and then the Fs generally rise after the increase in productivity takes effect. The Fs for the longline, dive and pot fisheries reach the levels of those in the "economic" strategy. Under a fall in productivity the solution once again begins by tracking the "ecological" strategy. Interestingly, even though the absolute F values continued to remain low after the conditions changed (all but the dive fishery remaining closer to the "ecological" than the "economic" strategy), they do increase in relative terms (rising by between two and tenfold). It is unclear exactly why this occurs. However, one suggestion is that in finding the Fs for the second half of the split-policy, the optimisation is responding to the increase in biomasses that occur as a result of the low Fs set in the first half of the policy and raises Fs accordingly.

One clear result emerges from comparison of the overall catch and objective function values for each of the runs, as well as the ratios of instantaneous catch, value and biomass at the beginning and end of each run. The effects of the change in productivity all but overwhelm any due to the fishing strategies implemented. If productivity rises, then all these summary statistics rise too, regardless of the strategy. Similarly, if productivity falls then all the summary statistics fall whether an "economic" or "ecological" strategy is implemented. However, the effects of the policies are not completely subsumed by the effects due to the changes in nutrients. The "economic" strategies continue to produce total catches and values, for the entire period, that are appreciably higher then those produced by the "ecological" strategies. The disparities in the values are much more striking for the case where there is a drop in productivity. The "ecological" total catches are about a quarter and the total values are about a third of the "economic" ones. Under a rise in productivity the "ecological" total

catches are only 5 – 25% smaller, and the total value only 5 – 10% smaller, than those from the "economic" strategies. The values of the ratios of the instantaneous measures are not so neatly partitioned along policy lines. When there is a rise in productivity the three measures are similar for both the single solution policies and the split "economic" strategy, though the single "ecological" strategy is marginally lower. In comparison to these three policy outcomes, the split "ecological" strategy produces much lower values for all three indices. The similarity among the values is not surprising given the very similar Fs in each case. Moreover, the split "ecological" strategy actually results in the greatest general increase in Fs over the course of the run. Consequently, it yields the smallest increase in the three measures as the higher Fs mitigate, to a limited extent, the effects of the higher productivity. In those cases where the productivity drops, the effects of the change in productivity almost completely overwhelm the effects of the policies. The only values, for any of the three relative measures, which differ amongst the various policies are those for the ratio of catches. Both the split policies have a higher ratio of catch than the single policy cases.

"Optimal" policies implemented in nutrient models, with a change in nutrients

The split-policy Fs for both the nutrient change scenarios (rise and fall), identified in the ECOSIM policy analysis, are applied in BM2 and IGBEM. The biomass trajectories in IGBEM (Table 7.14a and b) do largely concur with those of ECOSIM, at least at a qualitative level, though ECOSIM tends to result in more extreme changes in biomasses (Table 7.14a). This is true for both the ecological and economically driven Fs for both of the nutrient cases. As with the comparisons for no change in nutrients, there are some differences in the biomasses predicted for a few of the groups that are treated differently in the various models.

The dynamics of the piscivores in the nutrient models do not closely match those

in ECOSIM, particularly for the "ecological" strategies under falling nutrients and the "economic" strategies under rising nutrients. In both of these cases ECOSIM predicts a large fall in biomass while the other models suggest a small to negligible rise. Once again, this appears to be due to the static representation of the birds, sharks and mammals in IGBEM and BM2. This combined with the changing fishing pressures helps to force all of the fish groups in a different direction to that of ECOSIM, with its dynamic handling of all groups. The effect is amplified by the differing stock recruitment assumptions used in the models. For instance, under either policy, the case of falling nutrients sees ECOSIM predict large falls in flatfish, whereas IGBEM and BM2 predicted modest rises in the long-term as their benthic prey groups only fell marginally and the final Fs are lower than current levels. The impact of the initially high F under the "economic" strategy soon disappears from the nutrient models due to their constant recruitment term. In contrast, for the herbivorous and planktivorous fish the same mechanism prevents the nutrient models from allowing the large increases in biomass that ECOSIM predicts, as the constant recruitment in the nutrient models does not allow for the positive feedback between stock size and recruitment. The models also differed with regard to the dynamics of the abalone biomass. While all the models produced similar outcomes in the case of the ecologically based Fs under decreasing productivity, this is not the case any of the other scenarios. This cannot be explained by the failure of the 'invertebrate fishing fix' employed in IGBEM, but apparently arises from the differences observed in the dynamics of the macrophyte groups. ECOSIM consistently predicts a much smaller change in these groups with changes in nutrients, which could be traced to a lack of a shading effect by phytoplankton and other suspended material in the ECOSIM model. It is conceivable that a mediation or forcing function could be built into ECOSIM to mimic this, but this was not attempted. These long-term predictions do not take into consideration interim stock dynamics due to the

Table 7.14: Changes in biomass that result from the implementation of the suggested optimal fisheries policies.

(a) The relative change in end-point biomasses (end biomass under new policies and nutrient change / end biomass in "base case"), for each of the three models under the ecological and economically based strategies.

	Nutrients Rise						Nutrients drop					
	Split Economic			Split Ecological			Split Economic			Split Ecological		
Group	**ECOSIM**	**BM2**	**IGBEM**	**ECOSIM**	**BM2**	**IGBEM**	**ECOSIM**	**BM2**	**IGBEM**	**ECOSIM**	**BM2**	**IGBEM**
Phytoplankton	6	0.2	3	5	1.5	5.5	0.15	1	0.5	0.2	0.8	0.5
Small zooplankton	7	2	2.5	7	2	3	0.1	0.5	0.5	0.1	0.9	0.75
Large zooplankton	8	0.75	1.6	6	1.5	2	0.1	1.5	0.9	0.1	0.8	0.9
Deposit feeders	4	2	2.5	4	2	2	0.5	0.5	0.75	0.5	0.75	0.75
Filter feeders	8	1.3	2	8	1.5	2	0.13	1.1	0.75	0.13	0.9	0.9
Infaunal predators	4	1	3	8	1	3	0.2	1	0.75	0.3	1	0.9
Epifaunal predators	10	1.2	2	10	1.2	2	0.1	0.15	0.2	0.1	0.75	0.3
Benthic grazers	0.5	4	0.1	10	0.3	0.1	0.7	3	1.2	2	2	1.3
Microphytobenthos	8	4	0.6	10	100	1	0.1	0.75	2	0.1	1.2	1.1
Seagrass	0.1	0.1	0.3	0.1	0.01	0.2	7	1.4	1.1	10	0.8	1.2
Macroalgae	2	1.5	5	10	1.5	3	0.1	0.2	0.01	0.1	0.01	0.01
Clupeoids	6	1.2	1.2	8	0.5	1	0.1	1.5	0.8	0.1	1	1
Flatfish	4	0.75	0.8	2.5	1.5	0.6	0.1	1.3	1.2	0.1	2	2
Piscivores	3	0.8	1	5	2	0.9	0.1	1.5	0.75	0.1	2	1.5
Mullet	1.5	2	1.5	4	1.1	1.2	5	1	1	10	4	1.5
Sharks	9	-	-	9	-	-	0.05	-	-	1.5	-	-
Detritus	2.5	2	2	3	2	2	0.5	0.9	1.5	0.5	0.13	0.75

(b) The direction of biomass change for the group once the nutrient and fishing policy changes have occurred ('/' stands for increase, '\' indicates a decrease and '–' represents no significant change). The lumping and association of groups noted for table 7.6 also apply here and sharks are given for ECOSIM.

	Nutrients Rise						Nutrients drop					
	Split Economic			Split Ecological			Split Economic			Split Ecological		
Group	**ECOSIM**	**BM2**	**IGBEM**	**ECOSIM**	**BM2**	**IGBEM**	**ECOSIM**	**BM2**	**IGBEM**	**ECOSIM**	**BM2**	**IGBEM**
Phytoplankton	/	\	/	/	/	/	\	-	\	\	/	/
Small zooplankton	/	/	/	/	/	/	\	\	\	\	\	\
Large zooplankton	/	\	/	/	/	/	\	\	\	\	/	\
Deposit feeders	/	/	/	/	/	/	\	\	\	\	\	\
Filter feeders	/	/	/	/	/	/	\	/	\	\	/	\
Infaunal predators	/	/	/	/	-	/	\	\	\	\	-	\
Epifaunal predators	/	/	/	/	/	/	\	\	\	\	\	\
Benthic grazers	\	\	\	/	\	\	\	\	-	/	\	\
Microphytobenthos	/	/	-	/	/	-	\	\	-	\	/	/
Seagrass	\	\	\	\	\	\	/	/	-	/	-	/
Macroalgae	\	/	/	/	/	/	\	\	\	\	\	\
Clupeoids	/	/	/	/	-	/	\	/	-	\	\	\
Flatfish	/	/	/	/	-	\	\	/	/	\	-	\
Piscivores	/	/	/	/	-	\	\	/	/	\	\	\
Mullet	-	/	-	/	-	-	/	-	-	/	-	/
Sharks	/	NA	NA	/	NA	NA	\	NA	NA	/	NA	NA
Detritus	/	/	/	/	/	/	\	\	\	\	\	\

split policy structure.

When the patterns of biomass change are considered (Table 7.14b) rather than the change in final biomasses, the observed biomass trajectories are similar under the various policies and nutrient conditions for the three models. The biomass trajectories corresponded for more than 91% of cases under ecologically based strategies, and for more than 96% of cases under economically based strategies. Of the three models, BM2 is the one that most often produces a different direction of change in biomass to the other two models.

The system indices (Table 7.9), in particular Total Biomass, reinforce the impression that ECOSIM is much more responsive than the other two models. The Mean Trophic Level indicated that as a whole the system usually shifts in the same way, for each of the models, as the policy and productivity changes came into effect. However, the bycatch groups that are taken in ECOSIM see its Mean Trophic Level for Catch drop slightly rather than rise slightly, as is the case for the other models.

Nutrient scenarios vs the results of the optimisations with a change in nutrients

Given the overwhelming impact of the productivity on the total values and catch, this section provides a comparison of the scenarios where there is a change in nutrients but no change in policy, with scenarios where the optimal policies under changing nutrients are found. Under each of the split policies, the mullets were less intensively exploited than in the "base case" (as the Haul seine had an $F < 1$). This allows mullet biomass to increase during the first twenty years of the simulation. This resulted in higher biomass when the productivity changes, which in turn impacts on the benthic primary producers and their biomasses. There are also impacts on other groups such as a few of the planktonic groups, which are not directly affected by the change in Fs. An interaction between the change in productivity and the Fs is possible, but the

exact mechanism is unclear.

Conclusions from fishing policy analyses

Analysis of the fisheries strategies reinforces the impression that ECOSIM is more sensitive to changes in nutrients, and that the nutrient models are more sensitive to changes in F. The analysis also highlights the fact that trophic models predict unexpected changes in species not directly impacted by fishing. Such effects cannot, of course, be predicted from single species models.

7.4 Discussion

It is now widely accepted that human activity has had a significant impact on biogeochemical cycles at local, regional and even global scales (Ver et al. 1999). One response to this realisation has been the call for an ecosystem perspective in assessing and managing human impacts such as fishing and nutrient discharge. Developing the tools to meet this challenge has proved demanding for scientists. Until recently, limitations in knowledge and technological limits in computing have constrained attempts to model marine ecosystems. Despite earlier attempts (such as Andersen and Ursin 1977) and derived methods (for instance MSVPA (Sparre 1991)), comprehensive marine ecosystem models have not been widely available until the last decade, and their utility as predictive tools is still questioned by many. This paper sheds light on at least one aspect of the "robustness" of ecosystem models, by comparing different models developed for the same marine ecosystem, and examining some of their policy implications.

Four general conclusions appear to emerge from the analyses reported in this paper (they have been summarised in Table 7.15).

Table 7.15: Summary of the major conclusions and supporting results from the three ecosystem models considered here.

Summary of Conclusions	Major Supporting Evidence		
	ECOSIM	**BM2**	**IGBEM**
Multi-species effects: Changes in biomass and productivity that single species models would not identify as they are due to interspecies interactions.	**Best multispecies example from each model:** The direct (bycatch) effect of fishing on top predators is compounded by indirect (prey removal) effects.	Benthic grazers rise despite an increase in fishing pressure (economic strategy).	An increase in Chl a as a result of increased fishing pressure on clupeoids.
Sensitivity to nutrients rather than fishing: Changes in nutrients have a much larger, and more widespread, impact than changes in fishing pressure	**Ratio nutrient/fishing pressure induced change in biomass for each model:** Approximately 1.5 to 60.	1.5 to >1000.	Approximately 1.5 to 20.
Choice of indicator groups: The dynamics of groups such as seagrass, sharks and chlorophyll a (as a proxy for phytoplankton) consistently characterise the behaviour of many other groups and may summarise wider system responses and changes.	**Linked pairs of Groups – Indicator reflecting the behaviour of those groups in each model:** Planktonic – Phytoplankton Benthic Herbivores – Seagrass Herbivorous Fish – Seagrass +sharks Other Fish – Sharks Harvested groups – Sharks Other Benthos – Phytoplankton Top predators – Sharks	Planktonic – Chlorophyll a Benthic Herbivores – Seagrass Herbivorous Fish – Seagrass + piscivores Other Fish – Piscivores Harvested groups – Piscivores Other Benthos – Chlorophyll a + detritus	Planktonic – Chlorophyll a Benthic Herbivores – Seagrass Herbivorous Fish – Seagrass + piscivores Other Fish – Piscivores Other Benthos – Chlorophyll a

Table 7.15: Continued

Summary of Conclusions	Major Supporting Evidence		
	ECOSIM	BM2	IGBEM
Robustness to model formulation: Many results showed qualitative agreement across models, but there were a few important differences. These differences usually occurred when one or the other of the nutrient models produced results that differed from results that held across the other two models.	**Groups for which the models do not all agree in each scenario***		
	Nutrients change: No conflict.	Nutrients change: No conflict.	Nutrients change: Change in macroalgae opposite to other models.
	F changes: No conflict.	F changes: When F rises detritus drops only in this model.	F changes: No conflict.
	Economic F: Detritus unchanged.	Economic F: Detritus drops.	Economic F: Detritus rises.
	Ecological F: Zooplankton unchanged, piscivores and seagrass drop.	Ecological F: Small zooplankton drop and large zooplankton rise.	Ecological F: Small zooplankton rise and large zooplankton drop.
	Split econ F and N rises: No conflict.	Split econ F and N rises: Phytoplankton and large zooplankton drop.	Split econ F and N rises: No conflict.
	Split econ F and N drops: Mullet rise only in this model.	Split econ F and N drops: Large zooplankton, clupeoids and piscivores rise.	Split econ F and N drops: Detritus rise sand benthic grazers drop.
	Split ecol F and N rises: Benthic grazers rise.	Split ecol F and N rises: Clupeoids drop.	Split ecol F and N rises: Flatfish and piscivores drop.
	Split ecol F and N drops: Microphytobenthos, clupeiods, flatfish and piscivores drop and seagrass rises.	Split ecol F and N drops: No conflict.	Split ecol F and N drops: No conflict.

* "No conflict" indicates that the model agrees with at least one other model for all groups.

Multi-species effects

One possible value of ecosystem models is in identifying impacts that other methods would miss. For instance, single species models cannot predict the potential fall in epifaunal predators and rise in benthic grazers that BM2 predicts would result from the "economic" strategy. This effect arises from a combination of direct and indirect multi-species interactions, and is in direct contradiction to what single species models would predict, given the drop in the direct harvesting of epifaunal predators and the rise in the targeting of benthic grazers under the suggested policy.

Sensitivity to nutrients rather than fishing

In looking for conclusions about the real system (Port Phillip Bay) that appear to be robust to model uncertainty, one result stands out. Given the enclosed nature of the bay and the stock structure for most of the fished species (few entirely "local" stocks), the bay is much more likely to respond strongly to the effects of eutrophication than to those of fishing. For all models, all system-level indices are more sensitive to a change in nutrients than to a change in F (Table 7.9). The bay's geography (large and shallow, with restricted oceanic access) is such that if nutrient inputs change significantly - especially if they reach the level where nitrogen disposal, by flushing and denitrification, is overwhelmed (Murray and Parslow 1997) - the entire system can be quite heavily impacted. This scenario occurs when nutrients are increased by fivefold, though the increase in the biomasses of the higher trophic levels is probably overstated in ECOSIM. Extensive impacts as a result of large changes in nutrients have been found to be true of other models of Port Phillip Bay (Murray and Parslow 1999a), not just the ones discussed here. Such impacts also have the potential to be quite long-lived (chapter 2). This is due to positive feedbacks involving denitrification (Murray and Parslow 1997, 1999a), the immense nitrogen reservoir in the bay's sediments, and the apparent

dominance of a detritus based, rather than a more traditionally recognised primary production based, food web (Harris et al. 1996, chapter 2).

Turning to impacts of fishing, many of the finfish species recruit, at least in part, from externally based reproductive stocks (Gunthorpe et al. 1997). This means that at least some of the effects of fishing within the bay may be limited, so long as the external stocks are healthy. Although all three models showed less sensitivity to fishing than to nutrient impacts, there are notable differences between the nutrient models and ECOSIM that are attributable to model structure and assumptions. The damping of responses to productivity by the constant recruitment term in the nutrient models does suggest that it may play a significant role in compensating for changes in F. Despite this stabilizing feature in the nutrient models, substantial shifts in the Fs still result in corresponding shifts in the local population sizes of the target species, their competitors, predators and prey. For example, such impacts can be seen in the change in the biomasses of the flatfish, epifaunal carnivores, sharks and deposit feeders across the three models under the "economic" strategy. In general, impacts of fishing are likely to be greater on species that recruit locally, such as snapper (Coutin 1997, Gunthorpe et al. 1997), than on species that recruit principally from outside the Bay (for example King George whiting (Gunthorpe et al. 1997, Smith and MacDonald 1997)).

This phenomenon, whereby anthropogenically induced changes in nutrient status dominate over the effects from fishing, is not unique to Port Phillip Bay. Worldwide, many semi-enclosed bays have seen nutrient impacts overwhelm or modify the impacts from fishing (Caddy 2000). As Caddy points out, these nutrient impacts on marine catchment basins make integrated management essential, as fisheries management alone cannot address the problems.

Choice of indicator groups

Another general result of interest is that, across the range of management objectives and fishing and nutrient pressures imposed upon the ECOSIM model of Port Phillip Bay, only three qualitatively different system states arose. Moreover these system states can be characterized by the status of a few key groups. Given the increasing management interest in identification of indicator species, it is notable that a small group of species is sufficient to broadly characterise these three states. Using the sharks as an indicator group, the three states are characterized by:

- The biomass of sharks declining to negligible levels. This characterizes a fishing policy heavily influenced by economic objectives and/or a drop in the system's productivity (nutrient input).
- Sharks persisting at about the current levels of biomass. This characterizes a system free from recent extensive productivity shifts. It also arises from a fishing policy which attempts to find a compromise between ecological and economic objectives, although it is not clear that a deliberative strategy of this sort is the cause of the current state of the resources in PPB itself.
- The biomass of sharks increasing. This reflects a fishing policy guided primarily, or entirely, by ecological objectives and/or a wholesale rise in the system's productivity (though not to the point where the system is highly eutrophied as ECOSIM is currently unable to capture the indirect effects of changes in the nutrient and denitrification based system dynamics)

The persistence of the three system states across a range of refuge parameter settings, management objectives and environmental scenarios, in conjunction with the lack of response to fishing by many ancillary or lower trophic groups, does seem to result from the nature of the bay as discussed above. It is perhaps not surprising that a bay with as many in-built buffers as PPB has only a few "managed system" states where it is stable,

requiring quite large perturbations to push it from one state to another.

Despite the generalization noted above, the sharks alone do not summarize the entire state of the system under all policies and environmental changes. However a set of indicators comprising chlorophyll a, seagrass and sharks captures most of the effects, and changes in these indicators do seem to provide a warning that larger changes in the state of the system may have begun. Chlorophyll a is a much stronger indicator of the effects of changes in system productivity than any of the other groups and should be included in a set of indicators for that purpose. In contrast, the biomass of the larger fish, particularly sharks within ECOSIM, are good indicators of fishery based impacts on the system, though they also respond to changes in productivity. Seagrass is included in the list as it is particularly sensitive to changes in nutrient conditions, but is also impacted upon by the effects of fishing (either through habitat destruction or change in predation pressure). Thus between the three, they gave a good indication of what force is having the largest effect on the system and what overall state the system is in. It should be noted that this conclusion is limited to a "perfect information" case for a modelled system. In monitoring real systems in the field, a larger set of indicator groups may be more appropriate as they not only indicate change, but may also suggest some explanation of the cause. However it is encouraging that groups frequently referred to as being sensitive to change in nature are those which stand out as indicator species within the models. The loss of large shark species and the incursions of dogfish mark regime shifts in systems such as the Gulf of Alaska (Wright and Hulbert 2000) and the Grand Banks (Fogarty and Murawski 1998), while the loss of seagrass has been noted in many studies of impacted estuaries (Nienhuis 1983, Walker and McComb 1992). Chlorophyll a (as an easily measurable index of phytoplankton) is already used in monitoring for the effects of eutrophication (Harris et al. 1996) and is increasingly the subject of correlative studies with fisheries production (Lima and Costello 1995, Parsons and Chen

1994). Identifying species, or groups, which are persistently identified as being sensitive to changes in ambient environmental conditions and anthropogenic activities may be a first step to finding a set of useful indicators.

Robustness to model formulation

In spite of the qualitative agreement between the models at the broadest level, and the consistent form of the policy solutions found by ECOSIM, the differences in detail within and between the models also serve as a warning. For example, some of the policy conclusions from ECOSIM are found to be sensitive to the refuge parameters used. This underlines the requirement for analysis of parameter sensitivity regardless of the complexity of ecosystem models. Since completely inclusive, systematic sensitivity analyses are not possible for such models, a good understanding of likely key parameters is essential (chapter 1).

The results from this study also serve to underline the broader sensitivity to model formulation and approach. Formulation of multiple models, or at least multiple formulations of crucial mechanisms and processes, can identify groups that are sensitive to key assumptions. Substantial differences in some key groups have been demonstrated in this study in all three models examined. For example with the "economic" strategy and no change in nutrients, the interaction of the impact of fishing and the food web dynamics in the three models leads to three different patterns of change in the detritus. Given the long-term storage of nutrients that detritus represents in PPB, such a range of outcomes is a crucial result. While different models may agree qualitatively at the overall system level, management objectives are often concerned with particular groups and species, and conclusions about impacts on these can vary widely between model formulations (e.g. abalone).

However, a cautionary note must be sounded about the assumption that

conclusions that match across models are robust. While such an assumption is sound with regard to the assumptions that differ between models it cannot guard against the situation where the models share similarities in ecosystem structure and do not allow for processes which result in fundamental change to that structure. This is potentially one of the greatest problems facing "ecosystem" models. Where should the line be drawn, beyond which it is declared that model uncertainties and lack of process knowledge are too great to dare to use process-based models to extrapolate system state at the level of the entire system? This is a question that remains to be answered. For instance, the biogeochemical models employed here do a reasonable job of capturing the effects of mild to moderate eutrophication, but may well fail under conditions of extreme eutrophication (chapters 1 and 2).

7.5 Conclusions

Three further general points arising from this study are worth noting.

First, care needs to be taken in specifying objective functions for policy analysis. Clearly and not surprisingly, emphasis on economic objectives alone can result in systems that are very different from pristine. Perhaps more importantly, even where ecological criteria are included in the objective function, emphasis on particular groups (particularly the "charismatic megafauna" beloved of some conservation groups) can also result in systems that are far from pristine. The results in this paper suggest that focusing attention on the conservation of higher trophic groups does not produce a balanced system. A system populated only by those sub-webs featuring marine mammals is no more inherently balanced and representative than a system where they do not feature at all. Balanced objectives are not only required across sectors of human interest (say, economic and ecological), but also across the trophic groups that make up the systems being impacted.

Second, this study draws attention to an ongoing need to identify reliable means of synthesizing the often complex and voluminous information that can be produced by ecosystem models. A wide range of output indices have been presented in this study, including indices for individual groups as well as a few system-level indicators. None of these alone captures the key differences across policy options and forcing scenarios. On the other hand, a small set of key indices that can be intuitively and quickly grasped will be needed to communicate results to policy makers and decision makers.

Finally, while ecosystem models are emerging as key tools for investigating options for managing marine ecosystems, there is still much to learn about these tools. In this context, comparisons of predictions across alternative model formulations for the same system can be informative. The results from this study suggest that while some conclusions may be robust to model uncertainty, others clearly are not. While the use of ecosystem models for investigating management of marine systems has increased substantially in the last few years, there are as yet very few instances of multiple implementations for the same system. This study suggests that this comparative approach may lead to better understanding of key processes and assumptions in the use of these tools for ecosystem management.

Chapter 8 Effect of complexity on ecosystem models

Abstract

Ecosystem rather than species management has become an explicit part of policies that feature in international treaties and national legislation. Many of the tools that will be needed to fulfil the requirements of these policies are still in an early stage of development. One such tool is trophic ecosystem modelling. These models have been put forward as an instrument that can aid system-level understanding and provide insight into the potential impacts of human activities. Despite this, there are many gaps in our knowledge of their strengths and weaknesses. In particular, little is known about the effect of the level of detail in a model on its performance. There has been some consideration of the effects of model formulation, as well as the effects of physical, biological and chemical scope of ecosystem models on their performance. A review of existing research indicates that there is a humped relationship between model detail and performance, and that there are some guiding principles to consider during model development. Our review also gives some insight into which model structures and assumptions are likely to aid understanding and management, and which may be unnecessary. Further, it provides some understanding of whether some models can capture properties of real systems that other models cannot. The main recommendation is that, the use of a single "ultimate" ecosystem model is ill advised, while the comparative and confirmatory use of multiple "minimum-realistic" models is strongly recommended.

Keywords

biogeochemical, ecosystem, model, theoretical modelling, mass balance, complexity, model structure, model scope, model closure, multispecies

8.1 Introduction

During the last 30 years, every time there has been a major push to understand entire ecosystems, rather than isolated components, ecosystem models have become a popular tool (Watt 1975, Halfon 1979, Walters et al. 1997, Sainsbury et al. 2000). However, in the past complex general models have acquired a poor reputation, at least in some quarters, primarily because of two factors (Jørgensen et al. 1992). First, these models are often so large and complex that they are not necessarily cost efficient, with the majority of the modelling resources often spent in development and maintenance rather than on their application (Watt 1975). Second, complexity introduced for the sake of completeness accomplishes nothing if the resulting model is actually of poor quality (O'Neill 1975, Silvert 1981, DeCoursey 1992). While modern computing power makes ecosystem models attractive as computational restraints are lifted (Beck 1999), this does not solve the problems of uncertain model specification, parameterisation and system understanding, or the effects of model structure and detail on model performance (Silvert 1981, Jørgensen 1994). These areas of modelling still require much attention and the need becomes more urgent with increasing pressure on scientists and managers for "whole system" approaches, predictions and policies.

Ecosystem Models

Terminology associated with ecosystem models is confusing in that ecosystem models can refer to everything from total system models to models that focus solely on fisheries (the "top end" of the web) or water quality (the "bottom end" of the web). Here we use the term ecosystem model to refer to total system models rather than those multispecies models tied to one end of the food web or the other, which will be identified as water quality and fisheries multispecies models.

Within the last few decades, increasing computer power and a shift in the focus

of scientific and political thought has lead to a rapid growth in the number of multispecies and ecosystem models in existence (Silvert et al. 1981, Breckling and Müller 1994). For marine systems, the majority of multispecies and ecosystem models (a) use time-dependent differential equations, (b) conserve some currency (either biomass or nutrients), (c) concentrate on one part of the trophic web (either the nutrients and plankton, or the fish and other harvested species) and (d) separate physical and biological components and handle them in different ways. It is not surprising that the majority of published and applied multispecies models tend to concentrate on one end of the food web or the other, as the two main fields to embrace and make principal use of such models are fisheries and water quality. In both fields, the history of model development can be "characterised by the growing intricacy of their internal structure" (Fransz 1991). There have been a number of attempts at producing trophic ecosystem models for the marine environment, including: the cove model of Patten et al. (1975); the multispecies model by Andersen and Ursin (1977); the Fjord model of Bax and Eliassen (1990); ECOPATH with ECOSIM (Christensen et al. 2000); ERSEM I (Baretta et al. 1995) and II (Baretta-Bekker and Baretta 1997); and IGBEM and BM2 (chapters 1 and 2). Nevertheless, compared with the widespread use of water quality and fisheries multispecies models, the use of ecosystem models remains limited. As a result, there is still a lot of scope for the development of a thorough understanding of the implications of model structure on performance for these kind of models.

The various types of multispecies and ecosystem models each have associated advantages and problems (Table 8.1), but there is a list of features and potential drawbacks common to them all. In general, such models improve our understanding of systems by reflecting the two-way nature of system dynamics. Human impact on one part of a system can spread to other parts of the system, but system feedbacks and interrelations can also mean that an impact can have unexpected consequences even for

Table 8.1: Summary of the main strengths and weaknesses associated with the main types of multispecies and ecosystem models.

Model Type	Examples	Potential Strengths	Potential Weaknesses	References
Pelagic Pooled Ecosystem Models (or Water Quality Models)	NPZ, NPZD, FINEST	• Usually include environmental forcing • Some include environmental heterogeneity (though often only vertically) • Usually include constraints (via nutrient limitation) • Effects of formulation have received some attention • Some include size-age structure of all biological components (though may not always be justified)	• Ignore top-down effects from fish and fisheries (some even ignore zooplankton) • Can have a heavy reliance on source and sink terms • Tend to ignore benthic communities • May be steady-state or purely empirical	Fransz et al. 1991, Murray and Parslow 1997, Hollowed et al. 2000, Tett and Wilson 2000
Multi-species Models	Technical Interaction Models (TIM), Statistical Assessment Models (SAM), Multispecies Production Models (MPM), MSVPA, MSFOR	• Can usually account for age-size dependencies and temporal variation (except for MPMs) • Often include constraints (e.g. conservation of total biomass) • The effects of many underlying assumptions are well known	• Ignore bottom-up effects from lower trophic levels (e.g. primary producers) • Often ignore nutrient or environmental forcing • Some do not explicitly describe the trophic interactions (TIMs) or feedbacks (SAMs). • Often employ unsophisticated mortality terms • Can be sensitive to assumptions regarding recruitment	Hollowed et al. 2000
Biomass Size Spectrum Models		• Can incorporate the entire trophic web • Do not require extensive diet matrices as the only distinguishing characteristic used is size class (body weight) • Do not require extensive population or taxonomic data	• Assumptions with regard to feeding habits may not hold for benthic communities • Ignore influx due to reproduction and mortality other than fishing and predation • Mathematical properties of the underlying equations make them unsuitable for use over long time periods • Assume one preferred predator-prey weight ratio for the entire system • Often do not incorporate satiation or seasonality	Silvert 1996b, Duplisea and Bravington 1999

Table 8.1: Continued

Model Type	Examples	Potential Strengths	Potential Weaknesses	References
Static Aggregate Models	ECOPATH, Skebub	• Can make use of existing information and meta-analyses that would not be sufficient for intensive species based biogeochemical models • Trophic aggregation not consistent across the web (if aggregation is appropriate then this reduces the data needed for parameterisation) • Can incorporate the entire trophic web. • Constraints included (mass-balance, with the capability to build in biomass accumulation and depletion)	• Steady-state or instantaneous system state • Often use constant growth and production terms • Trophic aggregation not consistent across the web (this may affect results if aggregation is inappropriate) • Can be sensitive to diet-matrix used	Christensen et al. 2000, Hollowed et al. 2000
Dynamic Aggregate Models	ECOSIM, DYNUMES, ECOSPACE	• Trophic aggregation not consistent across the web (split-pool handling of groups is possible), which reduces data needs • Can incorporate the entire trophic web. • Forcing functions and trophic mediation functions can be applied • Use of predator-prey vulnerability parameters captures within pool heterogeneity with regard to predation (removes mass-action assumptions) • Constraints included (mainly via mass balance assumptions and predator-prey vulnerability)	• Seasonal behavioural changes difficult or impossible to incorporate • Can be sensitive to the value of the predator-prey vulnerability parameters • Trophic aggregation not consistent across the web (this may affect results if aggregation is inappropriate) • Often ignore environmental forcing. • Lack buffering against the effects of eutrophication	Christensen et al. 2000, Hollowed et al. 2000, chapter 7

Table 8.1: Continued

Model Type	Examples	Potential Strengths	Potential Weaknesses	References
Biogeochemical Total System Model	ERSEM, IGBEM, BM2	• Incorporate age-size dependencies for members of the higher trophic levels • Incorporate temporal variation and environmental forcing • Can incorporate the entire trophic web (in the form of functional groups) • Nutrient dynamics and recycling explicit. • Use of prey availability parameters captures within pool heterogeneity with regard to predation (removes mass-action assumptions) • Usually include spatial structure • Can have individual based components • Many constraints built in (e.g. nutrient limitation and predator satiation)	• Can be process and parameter intensive (therefore validation can be difficult and there can be large uncertainty, particularly in the benthic components) • Can be sensitive to assumptions regarding recruitment • Lack buffering against the effects of fishing • Lower trophic levels are represented by an aggregated pool per functional group, with no size or age structure (inappropriate if there are ontogenetic changes in habit or long generation spans)	Baretta et al. 1995, Baretta-Bekker and Baretta 1997, Hollowed et al. 2000, this thesis

those groups directly affected by anthropogenic activities (Hollowed et al. 2000, Mace 2001, chapter 7). There are also a number of potential problems common to multispecies and ecosystem models: (1) they often require more information than single species models (which has associated costs); (2) they are more prone to suffer from issues about optimal complexity (what should be included in the implementation and what should be omitted); (3) operational objectives and monitoring indices can be hard to define for the real systems to be modelled, and if indices are to be used to summarise model output then the problem of defining appropriate measures also arises for the models; and (4) there are often alternative hypotheses about system structure and function (Silvert 1981, Jørgensen 1994, Mace 2001). These features are particularly important when dealing with ecosystem models. However, as multispecies and ecosystem models are the only models with the potential to answer the environmental questions that single species and pure hydrodynamic models cannot (Hollowed 2000, Mace 2001), the advantages of the intelligent and attentive application of such models can outweigh their potential pitfalls.

One of the main criticisms aimed at ecosystem models is that their potentially immense complexity can make predictions highly uncertain (Duplisea 2000). If the model output is to be used directly to determine management actions (as in a fisheries stock assessment model), such a characteristic is clearly undesirable (Butterworth 1989). In contrast, when such models are used as a guide to possible impacts and to explore implications of alternative broad policies, this property is no longer such a problem. This is particularly true if the robustness of the conclusions is tested against a range of models incorporating different structural and parametric assumptions, representing a range of plausible alternative hypotheses about how the particular system may work. Such a comparative and confirmatory approach has many advantages as it allows for the identification of effects and policies robust across levels of complexity,

uncertainty and underlying system and model assumptions (Reichert and Omlin 1997, Duplisea 2000, chapter 7). Another related use for more complex ecosystem models is as a test bed for simpler models that may be used in assessment of the system, or part of it. Applying simpler assessment models to "data" generated from ecosystem models is a useful way of checking the robustness of the assessment models, and of identifying the circumstances in which it may be appropriate to use them for more "tactical" management advice.

Regardless of their potential drawbacks, ecosystem models have the potential to identify issues and causes beyond the bounds possible in single species models, or even multispecies models in some cases. Management strategies implemented to achieve a certain goal may have the opposite effect if multispecies or ecosystem considerations are not included. For example, without multispecies models, the potential of a seal cull to have an effect opposite to the one intended would be overlooked (Punt and Leslie 1995, Yodzis 2001a). Beyond even these multispecies considerations, without the inclusion of the links between the upper and lower ends of the food web and the forces driving them, erroneous conclusions may be drawn about environmental and anthropogenic impacts, as alternative explanations and scenarios are overlooked (Steele 1998, Yodzis 2001b, chapter 7). For example, a decline in the biomass of a herbivorous fish may indicate overfishing, but it may equally indicate degradation of their main food reserves as a result of eutrophication (chapter 7).

Unfortunately, although the need to integrate comprehensive biological, physical and chemical models is recognised, reconciling and reducing the dimensions of complexity required in each of the areas is an enormous and often poorly understood task (Mace 2001, Nihoul and Delhez 1998). Much of the handling of model complexity has been dealt with by drawing on experience from prior modelling efforts (Murray and Parslow 1997). As a result, the systematic understanding of the effects of model

structure and detail on the performance of ecosystem models is still at an early stage. There have not been many studies of the effect of model structure on marine ecosystem models. Unfortunately, this is a problem shared by the many branches of mathematical modelling (Brooks and Tobias 1996). Despite this, the study of model complexity in ecology can provide a sound point of departure for the study of the effects of the structure of ecosystem models on their performance. In turn, this can aid in understanding the mechanisms underlying the dynamics of real ecological systems.

8.2 A general history of the study of model complexity in ecology

Model aggregation

Optimal levels of model complexity, or appropriate degrees of trophic aggregation, remain a major problem in describing ecological systems. Thus, the study of the general properties of aggregation, and its limitations as a tool for use in model development and application, has received some attention in theoretical systems over the last 40 years. For instance, a number of researchers have considered the effects of aggregation from a theoretical standpoint and have produced some useful guidelines (Zeigler 1976, O'Neill 1979, O'Neill and Rust 1979, Cale and Odell 1980, Gardner et al. 1982, Cale et al. 1983, Iwasa et al. 1987, Bartell et al. 1988, Rastetter et al. 1992, chapter 5). The two most important rules that emerge to guide the use of trophic aggregation in model simplification are: (1) do not aggregate serially linked groups (predator and prey) (Gardner et al. 1982, chapter 5); and (2) do not aggregate species, age classes or functional groups with rate constants more than two- to three-fold different (Wiegert 1977, O'Neill and Rust 1979, Cale and Odell 1980, Gardner et al. 1982, chapter 5). Ignoring either of these guidelines is likely to result in a significant decline in model performance. Within the context of ecosystem models, this means that aggregating species to the level of functional groups is acceptable, but further

aggregation will lead to a model that performs poorly (chapter 5).

Construction rules

Generally most studies considering the complexity of ecological models have created (subjective) rules to apply during model creation and simplification to ensure that the most efficient model is employed (e.g. Innis and Rextad 1983). The most thorough of these was performed by Halfon (1983a,b) who used Bosserman's (1980) complexity measure ($\bar{c}$) to consider the effect of additional links between existing state variables (Halfon 1983a) and Hasse diagrams to investigate the structural properties of a number of different models (Halfon 1983b). Another notable, though more theoretical, approach was put forward by Iwasa et al. (1987). They gave formal mathematical rules that could be used to determine where aggregation of model variables was possible without loss of information. While these predominantly abstract theoretical and model development studies did present some examples with their discussions, they did not apply their methods to investigate the effects of complexity.

Formative studies of model complexity

Investigations of the effect of model structure on performance have usually occurred in less theoretical settings. One of the best analyses of the issues of model complexity and aggregation, and its impacts on subsequent management performance, was undertaken in the area of single species fisheries assessment and management. Ludwig and Walters (1981, 1985) demonstrated that for estimating the true optimal fishing policy a small and highly aggregated model can perform better than a more complex and "realistic" one, with the same fundamental structure, even if the "data" were generated using the more complex model. This has been attributed to the parametric sensitivity of more detailed models, and its potential to propagate errors,

which may mask the underlying contrast in the data and thereby create problems during parameter estimation (Iwasa et al. 1987).

This approach (comparing simpler "assessment" models against more complex ones) has subsequently been widely adopted in evaluating fishery harvest strategies, including stock assessment methods, mainly for single species management. This approach has been called "operational management procedures" (Butterworth and Punt, 1999) or "management strategy evaluation" (Smith et al. 1999) and has recently been extended to include evaluations involving multi-species interactions (Sainsbury et al. 2000, Punt et al. in press).

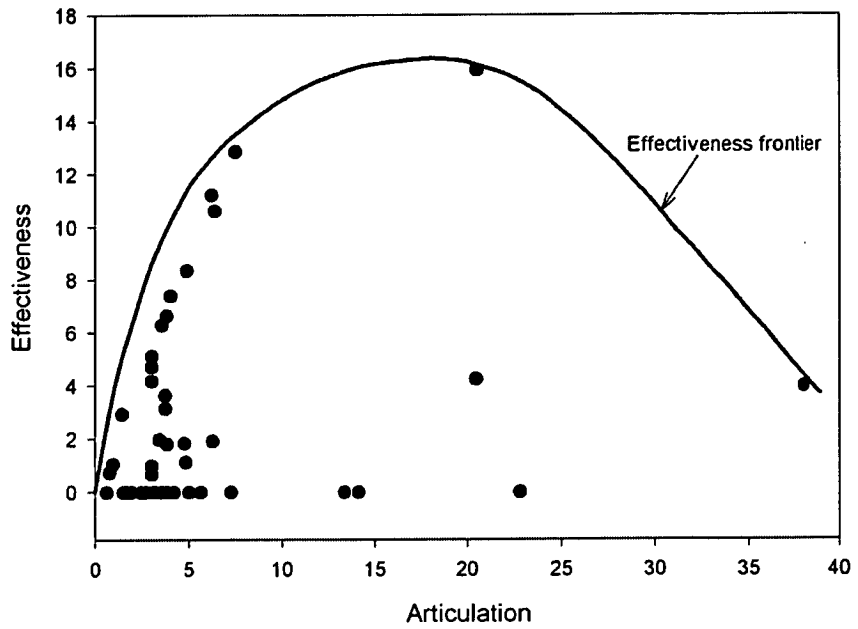
Within the more general ecological and ecosystem modelling literature, attempts to determine optimal complexity by comparing different models with each other or with data are scarce. Costanza and Maxwell (1994) began to span the divide between development and application when they examined the relationship between resolution and the predictive capacity of models – their discussion was based on the spatial dimension and was assumed to extend to the temporal dimension and number of components necessary. At the other extreme Kremer and Kremer (1982) and Hurtt and Armstrong (1996) both give examples of a search for optimal complexity through practical applications (they simplify or extend an existing model and discuss whether or not there is an improvement in performance). Overall, however, there are only a few attempts that take model performance into account while seriously considering the effects of model complexity on predictive models in a thorough or systematic way.

One of the earliest considerations of the structure of ecological models and its effect on model performance is the work by Wiegert (1975, 1977), who compared 5 models with differing trophic structure, levels of aggregation, spatial heterogeneity and formulation assumptions. The results suggested that the simplest of the models performed as well as the most complex, with a dip in performance for models with

intermediate levels of aggregation and simplification. This pattern of results was due to inadequate handling of spatial heterogeneity and time lags in the models with intermediate levels of complexity, whereas the simplest model did not require time delays and so that problem was avoided (Wiegert 1975). The modelling issues associated with varying degrees of model complexity in this study are strongly tied to the system being modelled and the modelling methods and assumptions employed. This may be why the relationship between complexity and performance observed by Wiegert (1975, 1977) is not reported in any other study considering the effects of model complexity.

The next major study to consider the effects of model complexity (Costanza and Sklar 1985) compared the predictive ability (judged against field data) of eighty-seven existing models of freshwater or shallow water bodies using three indices (articulation, accuracy and effectiveness). This work also found a non-linear relationship between model performance and complexity. The results were summarised in a plot showing that the relationship between effectiveness (explanatory power) and articulation (the amount of detail in conjunction with the physical and biological scope of the model) has a humped form (Figure 8.1). This finding supported anecdotal accounts from experienced modellers, particularly those that were involved in the International Biological Program of the early 1970s (e.g. Botkin 1977). One explanation for the shape of this relationship can be found in Jester et al. (1977). They suggested that at some point (as model complexity increases) the accuracy of the model reaches an asymptote, while the uncertainty continues to grow exponentially. Combining these into one plot of overall performance (incorporating accuracy and uncertainty) vs complexity gives the humped form found by Costanza and Sklar (1985).

Figure 8.1: Plot of articulation (measure of model complexity) against effectiveness (measure of model performance) for a number of existing aquatic models, redrawn from Figure 2 in Costanza and Sklar (1985).



The implications of data with a low signal-to-noise ratio

A different approach (a likelihood ratio test) was used by Yearsley and Lettenmaier (1987) to discriminate between three linear compartment models with varying levels of complexity (produced by aggregating compartments). The model comparison was made on the basis of synthetically generated data from a non-linear model of the global carbon cycle. They found that with realistic levels of measurement error even the most highly aggregated models are valid (a likelihood ratio test could not discriminate between even the most aggregated compartment model and the nonlinear model used to generate the "data"). Similar findings have also been reported for limnological models (van Tongeren 1995) and models of radionuclide transport in soils (Elert et al. 1999). These findings, that uncertainties in input data have a greater impact on the results than the model employed, are supported by the information theory concept of a model as a communication channel converting input data to output data. As

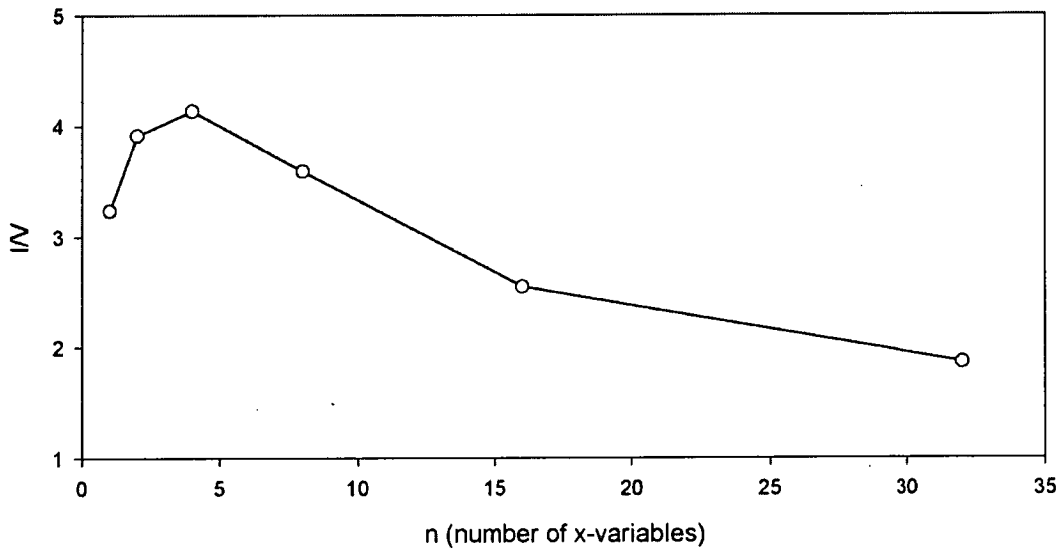
the signal-to-noise ratio of ecological and environmental data is typically low, there is no reason to expect that a large model spanning many noisy measurements will be any better than a model which deals with fewer, more precise, measurements (Silvert 1981).

Quantifying model complexity

One of the biggest problems in considering the effect of model structure on performance is how to quantify the amount of detail in the model (Costanza and Sklar 1985). Håkanson (1995) considered predictive ecosystem models for lakes and coastal areas and tried to compare empirical and dynamic models by first considering the r^2 values of a number of stepwise multiple regression models and then by examining the standard deviation of a number of additive and multiplicative models. Once again it was shown that there was a humped relationship between an indicator of performance and the number of variables included, though the peak of the plot was closer to the smaller model sizes in this case (Figure 8.2). Håkanson's (1995) work provides evidence (as does Costanza and Sklar (1985)) for the long held belief that predictive power increases quickly with the elaboration of simple models, but the trend is eventually reversed as accumulating errors and process and parameter uncertainty negate any potential benefits of increased detail. Extending this work, Håkanson (1997) defined a measure of predictive power (PP) of a model (based on the fit to multiple datasets) and used it to examine the predictive capabilities of models of the transport of radiocesium in lakes. The models considered included both empirical and dynamic models of differing size and complexity. This study also identified a humped relationship between predictive power and model size. More importantly, Håkanson (1997) gave another explanation for the decline in performance with increased detail. Accumulated uncertainty alone was not responsible for the drop. When it comes to using models in a prognostic sense, large models can be prescriptive rather than predictive (Håkanson 1997) - all the extra detail

can hardwire the responses rather than introduce flexibility. Further, Håkanson (1997) points out that the predictive power of a model is not determined by its strongest point, but by its weakest.

Figure 8.2: Plot of predictive power (I or r^2) / accumulated error (V or SD) against the number of x-variables (n) for predictive lake models, redrawn from Figure 6a in Håkanson (1995). I is the information value, V is the accumulated uncertainty (relative standard deviation = SD/MV), SD is the standard deviation and MV is the mean value.



The study of marine models

Regarding models of marine systems in particular, several researchers have considered how the form of parts of models (such as grazing and mortality) affect their dynamics (Steele and Henderson 1992, Edwards and Brindley 1999, Murray and Parslow 1999b, Gao et al. 2000), but only a few have considered how the structure of entire models influences their behaviour (Yool 1998, Nihoul 1998, Nihoul and Djenidi 1998, Hoch and Garreau 1998, Tett and Wilson 2000, Murray 2001, this thesis). The work of Hoch and Garreau (1998) and Nihoul's body of research (Nihoul 1998a and 1998b, Nihoul and Delhex 1998, Nihoul and Djenidi 1998), though primarily concerned

with complexity from a hydrodynamic standpoint, should be of interest to all ecosystem modellers. Their findings highlight that not only are ecosystem models hampered by the same issues of internal complexity as any model, but they must also find a balance (or trade-off) between their various physical, chemical, geological and biological features (Hoch and Garreau 1998, Nihoul 1998a).

Within the field of single species fisheries modelling there is a well-established methodology for addressing the issue of model complexity. The approach involves simulation testing the performance of simpler models against a more complex one, using the latter to capture some of the possible complexities of the real world. Essentially, the "testbed" model is a simulation model incorporating complex processes, thought to occur in nature, which acts as an artificial world. This artificial world (and the "data" it provides) then becomes a useful testbed against which to judge the performance of simpler models that display a range of structural complexity and form. The more complex "testbed" model is referred to as a "deep" model, while the simpler operational models are called "shallow" models. Therefore the methodology is referred to as "deep-shallow model comparison".

Given the signal-to-noise ratio of ecological data and what this may mean for model performance and interpretation, the use of the "deep-shallow" model comparison (as applied by Ludwig and Walters (1981, 1985) to fisheries science) is very attractive. The advantage of employing this methodology is that it allows the modeller to begin with a model that is known to work and then to "strip it back" to identify the level of detail that is effective and most efficient. Moreover, it provides a baseline of perfect knowledge (i.e. data generated by the deep model rather than gathered from the field) and therefore enables separation of the effects of model complexity due to model structure from those due to data uncertainty. Both sides of the problem must eventually be addressed, but keeping the two separate will clarify interpretation of any results.

Yool (1998), Murray (2001) and I (this thesis) apply the deep-shallow model methodology in a more general marine ecology setting. Yool (1998) decomposed the Fasham (1993) plankton ecosystem model and then reconstructed it stepwise in order to determine if a "best minimum model" existed. Murray (2001) compared a simplified version of the Port Phillip Bay Integrated Model with the original. Lastly, I compared a number of ecosystem models of varying degrees of detail and complexity. In addition I considered the effects of a range of simplifications or alternative assumptions on model performance. Each of these studies found that some degree of simplification (of structure, trophic coverage or physical scope) is possible without degrading the model, but simplifying too much leads to a substantial decline in model performance, particularly for the purposes of predicting the effects of changing conditions. While the study of the effects of the complexity of marine models as a whole is at an early stage, the work so far has provided some useful insights into two main areas of model construction and these are discussed in more detail below.

8.3 Model scope

The scope of a model is largely defined by its spatial resolution, the temporal spacing of output (the model equivalent of sampling frequency in the field), the nutrients that are represented explicitly, and the biological web that the model describes. Along with the particulars of model formulation (discussed below), model scope is potentially one of the most important aspects of model complexity. Computational demands and the logistical requirements associated with collecting sufficient information to parameterise and validate ecosystem models are one of their biggest drawbacks (Silvert 1981, Sugihara et al. 1984, Lee and Fishwick 1998). Simplifying the biological or physical scope can make a model much easier to construct, summarise and interpret. The problem is that removing too much detail can leave a model that is simple

to parameterise and quick to run, but that has limited prognostic use (Tett and Wilson 2000, Murray 2001, chapters 4 and 5). The challenge is to define an optimum scope that minimises complexity, but which facilitates valid and robust predictions.

Trophic complexity

The trophic complexity of a model is concerned with two aspects of model structure, the number of trophic levels explicitly represented in the model and how these levels are divided into species or functional groups (Murray and Parslow 1997, Pahl-Wostl 1997). It is understandable that multispecies models concerned primarily with water quality or harvested species may not include all trophic levels, but this assumes that groups at one end of the web don't significantly influence the behaviour at the other. In ecosystem models that may be used to consider many alternative anthropogenic scenarios, or the direct and indirect effects of processes such as fishing, the representation of a greater number of trophic levels is probably required. Unfortunately, the problem of where to draw the line remains an issue as every additional group included increases the complexity, modelling and data requirements. It may be desirable to truncate the web and omit the top predators, but the way this is done can strongly influence model behaviour (chapter 6). This aspect of the problem is discussed below in the context of model closure.

The number of species or functional groups (as defined by size classes, feeding linkages, shared predators and life history strategies) represented in a model needs careful consideration. Species level detail could mean the complete collapse of many biogeochemical ecosystem models and is beyond what is possible based on collected data from many systems. Nonetheless, without the flexibility inherent in a trophic web rather than a chain, realistic dynamics, especially under changing conditions, may be very difficult to capture (Baretta et al. 1995, Pahl-Wostl 1997). Thus, the systematic

consideration of the effects of trophic complexity on model behaviour is an important concern.

Randomly constructed food web models have been investigated by many researchers (Gardner and Ashby 1970, May 1973, Siljak 1974 and 1976, Waide and Webster 1976, Pimm and Lawton 1978). Within the context of ecosystem models however, consideration of realistically structured webs is more enlightening (Bosserman 1982). Consideration of changes in the behaviour of models with realistic web structure when the web is simplified by aggregation or omission of groups indicates that simplifying trophic structure too much is rarely beneficial (Christensen 1992, Sugihara et al. 1984, Optiz 1996, Pahl-Wostl 1997, Yool 1998, chapter 5). The simplified webs, especially those reduced to less than 25% of the size of the original model web, are not able to represent enough of the processes and interactions in the system to faithfully reproduce system dynamics, particularly when the strength of environmental or anthropogenic pressures change (chapter 5). This finding may also give some insight into the effect of a loss of biodiversity in real ecosystems. If real ecosystems respond to the loss of species or functional groups in the same way models do then it is likely that the impacts of a loss of biodiversity will be minimal if non-critical groups and interactions are lost and ecosystem conditions do not change. However, the magnitude of the impacts is much larger if conditions do change, as a result of environmental forcing (e.g. ENSO) or anthropogenic activities. This agrees with the ecological insurance hypothesis (Yachi and Loreau 1999), which proposes that diversity provides natural communities with a buffer against change.

As with the relationship between model performance and structural detail in general (Figure 8.1 or 8.2), there appears to be a nonlinear relationship between trophic complexity and behaviour. This relationship can be of two forms. It can be humped, like the overall relationship (Bosserman 1982, Gardner et al. 1982, chapter 5) or it can be in

the form of a threshold-triggered step-function (Tett and Wilson 2000, chapter 5). The second of these relationships is less common and is tied to groups with critical ecological roles, which must be explicitly represented to capture correct system dynamics.

Connectance (MacArthur 1955), the ratio of the number of strong:weak interactions in the web (McCann 2000) and redundant groups (Yachi and Loreau 1999) have all been proposed as explanations for the patterns of change in model dynamics with varying levels of trophic complexity. However, the work by Yool (1998), Edwards (2001) and the work presented in chapter 5 suggests that none of these alone can explain the patterns of performance observed and that the identity of the components and links included can be the most important determinants of performance. Thus, as with any other kind of model, it is far more important that crucial system characteristics are captured rather than rote application of a set of "modelling rules". The findings given in chapter 5 also have important implications for the debate within ecology about whether increased diversity stabilises (MacArthur 1955) or destabilises (Gardner and Ashby 1970) an ecosystem. Many theories put forward in this debate assume a linear relationship between diversity and stability, but the relationship observed in the work on ecosystem models presented in chapter 5 is nonlinear. This suggests that there is no simple relationship between diversity and system behaviour and stability.

Simple rules may not always be guaranteed to work, but they may still prove to be useful. Within the context of ecosystem models and trophic complexity, the finding that over-simplifying is not usually advantageous is probably the strongest and most useful guideline for model development. One way in which this is exemplified is the effect of trophic aggregation on model behaviour. While aggregating species with rate constants that differ by less than threefold, which also have similar or common predators and prey, into functional groups is a successful modelling technique, pooling

functional groups is less successful than omitting the least important functional groups entirely (chapter 5). This stems directly from the guidelines given by the general papers on the effects of model aggregation mentioned above (Wiegert 1977, O'Neill and Rust 1979, Cale and Odell 1980, Gardner et al. 1982) and is shown explicitly in chapter 5. The other general guideline to come from studies of model complexity deals with the use of empirical submodels in the place of important, but poorly known, or omitted, processes, groups and linkages. This will be discussed in the section on model formulation below.

Nutrients included explicitly in models

Tett and Wilson (2000) advised that ecosystem models should be biogeochemical, as they must conserve one or more elements so that the potential growth of groups can be capped. The success of ECOSIM models (Walters 1998) suggests that conservation of biomass may also be sufficient.

In biogeochemical models, it is quite common to use the most limiting macronutrient (carbon, nitrogen or phosphorous) as the model currency and assume that the conversion of the other nutrients conforms to the Redfield ratio (Murray and Parslow 1997). However, this approach does not allow the model to adjust to spatial and temporal differences in nutrient availability (Baretta et al. 1995). This inability should not present a significant problem and will not (in general) lead to large model divergences if the system state is mesotrophic to eutrophic. This is because the other nutrients should remain in excess, even if not exactly in Redfield ratios. However, when a system is in an oligotrophic state the dependence of the model on a single macronutrient currency can be a problem (chapter 7). Under these conditions the identity of the limiting nutrient may well change and the preferential remineralisation of nitrogen and phosphorous will cause significant departures from the Redfield ratio, with

potentially catastrophic implications for production estimates and the dynamics of transmission up the food web. The successful application of models such as ECOPATH with ECOSIM to the open oceans (Christensen et al. 2000) suggests that models employing the conservation of biomass may not suffer as much from this problem. However, environmental influences are not usually present in such models, and if they are they are usually in the form of prescribed forcing functions (Hollowed et al. 2000). If environmental conditions became a more integrated part of these models, then the problems observed in biogeochemical models may appear in models like ECOSIM too, but this remains to be seen.

Physical scope

The last important aspect of model scope that can affect model behaviour is the physical scope of the model, and in particular the spatial resolution of the model. Many multispecies and ecosystem models (e.g. mass balance aggregate system models such as ECOSIM) do not include any explicit spatial representation. However, space is a vital system resource in its own right in many marine systems and as such the way in which it is represented can have a significant impact on model dynamics and predictions (Murray 2001, chapter 4). Many of the model stability issues identified in ecological and ecosystem models in the past (May 1974, Pimm 1982, Cohen and Newman 1988, Christensen et al. 2000) disappear with the introduction of explicit spatial (and thus environmental and/or ecological) heterogeneity (Johnson 1997, chapter 4). This assertion does not only apply to biogeochemical ecosystem models (like those employed in chapter 4), but extends to other types of multispecies and aggregate system models (like ECOSIM). There are many examples of these models being explicitly (through the development of ECOSPACE (Walters et al. 1999)) or implicitly (by separating individual model groups into inshore and offshore components (Christensen

pers. com.)) expanded to incorporate spatial partitioning. This is not to say that ecosystem models must be tied to general circulation models. Such a move would be computationally prohibitive and probably of little assistance. The box-model approach to transport processes is useful as it neglects small-scale gradients, but still allows for regional differences and spatial self-structuring which, in turn, lead to the formation of distinct communities and ecological zones (Baretta et al. 1995, chapters 1 – 3). Even when using box-models, large numbers of cells may not be necessary. For example, the work presented in chapter 4 shows that an 8-box model was a good compromise between the computational intensity associated with a 59-box version and the trophic self-simplification and degradation in performance associated with 3- and 1-box versions of the same model. This is another facet of model structure where intermediate complexity is best.

8.4 Model Formulation

The main concern of the majority of model studies considering the effect of model structure is model formulation not model scope. The way in which a model is implemented can have a large impact upon its performance and usefulness (Silvert 1981). The key areas of model formulation which have received some attention for marine system models concern process detail (particularly with regard to grazing functions and mortality terms) and the role of empirical submodels and forcing.

Process detail

Whereas physical oceanographers have a set of "basic hydrodynamic equations" there is no such set of equations in ecological modelling (Tett and Wilson 2000). The problem is compounded in ecosystem models, as the modeller must integrate a variety of processes and interactions with differing characteristic temporal and spatial scales

(Barthel and Goñi 1995). Consequently, ecosystem models run the very real risk of incorporating too much detail to be comprehensible, or over-compensating in the other direction and not including enough to be realistic or of any real use. Given this risk, and the increasing number of ecosystem models, there has been surprisingly little published on the effects of formulation detail on the dynamics of ecosystem models. Moreover, despite the contention that confirmatory and comparative model studies show the greatest promise for guiding management decisions, there have been few studies to compare different forms of ecosystem models (chapter 7).

Specific aspects of the effect of process detail will be discussed in the following sections, but there are some pertinent observations about overall detail that arise. The work by Håkanson (1997) and I (chapters 2 and 3) indicate that highly detailed, often physiologically based, process detail is not a pre-requisite for a successful ecosystem model. In chapters 2 and 3, I compared the outputs and predictions of two ecosystem models that covered the same web and processes, but with differing levels of process detail. The Integrated Generic Bay Ecosystem Model (IGBEM) is highly physiologically detailed, while Bay Model 2 (BM2) uses the same functional groups, but much simpler assimilative equations. It was found that, with regard to understanding system dynamics and qualitative responses to changing conditions, BM2 can represent systems as well as IGBEM and in some cases the performance of BM2 is better than that of IGBEM. In comparison with real bays, the predictions from BM2 are better than those from IGBEM in the areas of microfaunal dynamics, relative community composition, size structure, and sediment chemistry. IGBEM is better for biomass and consumption estimates of some groups, such as zooplankton, the ratio of chlorophyll a to dissolved inorganic nitrogen in the water column and for robust dynamics across a wide range of nutrient loadings. BM2 does have some weaknesses related to its simplified form: it is more sensitive to parameter values than IGBEM; the detritus

feeding benthic groups and microphytobenthos occasionally show almost exponential growth (suggesting the lack of a limiting factor for these groups, such as the availability of space); and the assumption that nutrients are always in Redfield ratios causes BM2 to perform poorly in oligotrophic conditions (where this assumption is often violated) (chapters 2 and 3). Despite these weaknesses, the overall performance of BM2 is as good or better than IGBEM and this shows that physiological detail is not necessarily required and that simpler formulations can work. This is a boon given that when using BM2 instead of IGBEM the number of parameters required drops by more than 50% and the computational demands also decline substantially (the run time drops by 30 – 60 %)(chapter 2). The amount of process detail required is only as great as that needed to successfully capture crucial system dynamics. The findings of Håkanson (1997) reinforce this assertion. In that study the simpler model had the most predictive power and the more complex the least.

The work of Tett and Wilson (2000) cautions against taking the process of simplification too far. They found that models that sacrifice large amounts of biogeochemical or ecological detail in favour of the other cannot adequately describe the dynamics of the plankton. A minimum level of both biogeochemical and ecological detail is required. The research of Murray and Parslow (1999b) and Murray (2000) arrives at a similar conclusion. They found that a much simpler model compared favorably with a more complex model of the same system, but with some caveats. This made the simplified model an excellent aid in the development of a more sophisticated model, but the inability of the simple model to capture certain dynamics in some conditions meant that it could not replace the sophisticated model. The extra detail of the larger model was required for fully informed system management and to allow scientists and managers to understand and consider a number of alternative scenarios. Håkanson (1997) considered the effects of complexity on performance by sequentially

increasing the detail included in the models considered, rather than systematically reducing detail as in this study. However, Håkanson's (1997) findings about the minimal realistic model also indicate that the "correct" level of process detail is that needed to successfully capture crucial system dynamics.

These studies on the "correct" level of process detail needed in ecosystem models may also be instructive when considering the dominant processes in real ecosystems. It is likely that the processes required in models to successfully capture crucial system dynamics are the dominant processes structuring systems. Furthermore, consideration of the dynamics displayed by ecosystem models may further the understanding of the behaviour, or potential behaviour, of real ecosystems. For example, even ecosystem models that do not incorporate detailed representations of physiological processes (e.g. BM2) can produce runs which show major transitions in system state (where some groups with high biomasses in one state decline to much lower levels in the other state and vice versa). In real systems the occurrence of such events are assumed to be linked to anthropogenic activities or changes in external forcing, but in ecosystem models they can occur even in the absence of these factors. This suggests that at least some of the transitions in system state observed in real systems may be emergent behaviour caused by internal system interactions or resource dynamics rather than the result of some external force.

Studies comparing the performance or predictions of different types of model are useful for judging how robust general findings are to the underlying assumptions of the models (chapter 7). However, they are also an excellent source of information on the effects of process detail on model dynamics. Duplisea and Bravington (1999) found that the results from a length-cohort model very similar to a MSFOR (multispecies forecast model) and a size-spectrum mass transfer model both lead to the same conclusions regarding fisheries management strategies. Thus, within the context of the system

dynamics related to the particular question of interest, the explicit process detail of the MSFOR did not confer any advantage over the far simpler size-spectrum model. In general, size-spectrum models are a successful methodology, at least for pelagic aquatic ecosystems (Silvert 1996b). However, in the context of the evaluation of management strategies Duplisea and Bravington (1999) recommend a few modifications, such as allowing some disaggregation into functional trophic-groups and including more realistic grazing terms. The popularity of ECOSIM suggests that it may also be a successful methodology. This is supported by the finding given in chapter 7 that, with a few exceptions, ECOSIM gave the same qualitative predictions as the biogeochemical ecosystem models IGBEM and BM2. The differences observed stem mostly from the lack of spatial detail in ECOSIM, or parts of the web that are poorly known. The main differences between the biogeochemical models and ECOSIM that are a direct result of model formulation are that the biogeochemical models are not as buffered against changes in fisheries as ECOSIM is, but they are more buffered against changes in nutrient loading. This is a reflection of the more realistic behaviour of the low to middle trophic groups in the biogeochemical models, whereas the higher trophic groups react more sensibly in ECOSIM (chapter 7). This is not surprising given their respective development histories and structure, but does caution against the assumption that a formulation that works at one level will work for every level.

Grazing terms

General ecological research, as well as the results of more directed marine modelling, has shown that the form of grazing terms used can have important effects on overall model behaviour and predictions (May 1976, Hassell and Comins 1978, Begon and Mortimer 1986, Steele and Henderson 1992, Tett and Wilson 2000, Gao et al. 2000, chapter 6). Evaluation of the effects of the functional response used in plankton models,

built around relatively simple food chains, indicated that they do not have as great an impact as other parts of the model (Steele and Henderson 1992, Murray and Parslow 1999b). In contrast, consideration of the effect of the grazing terms used in a total system model, with a complex trophic web, (BM2) in chapter 6 indicates that they can have a substantial impact on model behaviour. In chapter 6 I concluded that, while there are biologically and mathematically sound arguments for the inclusion of sophisticated and dynamic functional responses, the extra parameterisation is not justified because the Holling "type II" response predicted the same general patterns of behaviour, and thus the same conclusions about system dynamics. Nevertheless, it is also stressed that very simple responses (such as the Holling "type I") do not allow for realistic dynamics over the range of conditions of most interest in system management scenarios. Tett and Wilson (2000) reach a similar conclusion, whereas Gao et al. (2000) conclude that the optimal functional form will depend on the specific study and that more observations and understanding of real marine systems are required before the matter can be clarified. The latter may well be true, but for models incorporating a realistic food web, simpler grazing terms may suffice due to the many other stabilising features inherent in the web (Tett and Wilson 2000).

Model closure

The other main aspect of model formulation that has received explicit attention is the form of model closure (Steele and Henderson 1992, Edwards and Brindley 1999, Murray and Parslow 1999b, chapter 6). Model closure refers to the form of the mortality term applied to the top most group(s) explicitly included in the model. Linear and quadratic mortality terms are the most common means of dealing with model closure and these reflect the cases when the effect of predators not included in the model are assumed to either be constant (linear mortality) or to change (quadratic mortality) with

the population of their prey (the top most modelled group(s)). The specific form used can have a substantial impact on model behaviour (Murray and Parslow 1999b).

Steady-state analysis of simple food chain plankton models indicates that model closure can be the most important determinant of model behaviour (Steele and Henderson 1992, Edwards and Brindley 1999, Murray and Parslow 1999b). In contrast, its effect on a total system model (with a complex trophic web) shows it is much less important than other aspects of model structure (chapter 6). However, even in the case of the total system model the need for the representation of higher predators (either explicitly or implicitly via quadratic mortality terms) is recognised. Unfortunately, conflicting conclusions regarding the dynamics of the highest predators (sharks, mammals and birds), when there are large changes in conditions and differential stability of the various forms of closure across a range of conditions, mean that further work on this topic is necessary (chapter 6). Nevertheless, it seems likely that, as a general guideline, the use of quadratic closure is acceptable regardless of the size of the implemented web (chapter 6).

Forcing functions and empirical submodels

The last facet of model formulation that has received some attention, is the value and usage of empirical formulations. Empirical formulations (or empirical models as they are also known) are functions that describe observed patterns or relationships in data, but without trying to capture real process dynamics. These formulations have both advantages and disadvantages. They can be developed without much understanding of the phenomenon of interest, they are simple (as they do not need to include complex causality) and they can be developed rapidly (DeCoursey 1992). All of these features make empirical models attractive, and within their range of applicability they can often provide better predictive power than dynamic models (Håkanson 1997). Their limiting

feature is that many domains of interest can be outside the range of applicability. This, along with the arbitrary nature of these models and the associated risk of adopting a misleading approach or false assumptions, can mean they are less than ideal (DeCoursey 1992).

Within the realm of marine ecosystem models, the choices are more complex than empirical *vs.* purely process models. The two approaches usually have different purposes and often complement rather than compete with each other (Håkanson 1995). Moreover, empirical models can play a role within dynamic process models. Given that the understanding of some components of marine ecosystems are poor (e.g. the processes and forces shaping the behaviour of the benthic infauna) and that a model is only as strong as its weakest part, the use of empirical submodels for the least known parts of the system is an attractive alternative. The inappropriate use of simple forcing functions can lead to very poor model performance, while the use of a structured empirical submodel can work very well (chapter 5). Such a submodel can compensate for not explicitly representing a poorly, or incompletely, known component, which has a potentially crucial role in the modelled system. For example, in the empirical model of nitrification-denitrification by Murray and Parslow (1999a) the amount of ammonia available for nitrification-denitrification was calculated using a temperature-dependent rate of breakdown of the form

$$R_X = \Phi \cdot X \tag{8.1}$$

where R_X is the ammonia released by remineralisation of component X, Φ is the temperature-dependent rate of breakdown for the component X and X stands for labile detritus (DL), refractory detritus (DR) or dissolved organic nitrogen (DON) in the sediments. This available ammonia is then used in the following nitrification (S_{NIT}) and denitrification equations (S_{DENIT})

$$S_{NIT} = R_{NET} \cdot \theta_{DMAX} \cdot \boldsymbol{max}\left(0, 1 - \frac{R_{NET} \cdot \gamma_{SED}}{r0}\right) \quad (8.2)$$

$$S_{DENIT} = S_{NIT} \cdot \boldsymbol{min}\left(1, \frac{R_{NET} \cdot \gamma_{SED}}{\theta_{rD}}\right) \quad (8.3)$$

where θ_{DMAX} is the maximum rate of denitrification, θ_{r0} is the temperature-dependent minimum rate of respiration that supports nitrification, θ_{rD} is the peak of the nitrification-denitrification curve (as defined by Murray and Parslow 1999a), γ_{sed} the depth of the sediment layer considered in the model and R_{NET} is the total available ammonia, which is given by

$$R_{NET} = \boldsymbol{max}\left(0, R_{DON} + R_{DL} + R_{DR} - P_{NH,MB}\right) \quad (8.4)$$

where $P_{NH,MB}$ is the amount of ammonia in the sediments taken up by microphytobenthos for growth. This empirical model performs well and is robust (Murray and Parslow 1999a), but it is not interactive, in the sense that it is not dependent on the activity of the benthic groups included in models with more complex trophic structure. Therefore, modifications were made to allow it to be interactive when it was included in the ecosystem model BM2. In BM2 the amount of ammonia available for nitrification and denitrification is determined by the activity of the attached bacterial populations and other sediment dwelling fauna and flora (chapter 2). Nitrification and denitrification is then completed using the empirical formulations of Murray and Parslow (equations 8.2 and 8.3 above). This empirically based bacteria-denitrification submodel is an improvement over the purely empirical model of Murray and Parslow (1999a). It was also a vast improvement over other process based attempts at modelling bacteria and denitrification (chapter 1), subjects that are still poorly known in many respects. Thus, the use of an empirical representation of an important process can prevent degradation of model performance. This is especially true if the causal mechanisms for the process are poorly known, or if explicit inclusion of the details of

the mechanism is beyond the scope of the model or the capability of the available data or computational resources.

8.5 Model performance under changing conditions

Using ecosystem models to gain insight into a system and indicate (at least) qualitative trends associated with a change in "forcing" conditions is one of their most useful roles. It is also at this point that assumptions underlying the model formulation can have their greatest impacts. Thus, confirmatory comparison of models is strongly advocated. A comparison of three ecosystem models (ECOSIM, BM2 and IGBEM) in chapter 7 indicated that overall model structure and formulation can be robust (i.e. provide the same general predictions) under changing conditions, but still predict some potentially important differences in specific cases. For example, applying a fisheries management strategy developed purely to maximise economic gains to all three models produced predictions that coincided for the majority of the biological components in all the models and there was agreement between at least two of the models for all the components except detritus. The three models all gave different results for detritus (ECOSIM predicted no change, BM2 predicted a decline and IGBEM an increase). Given the role of detritus as a long-term storage of nutrients in enclosed bays like the one modelled, such a range of outcomes is a crucial result. This illustrates how conclusions drawn from different models can be very different for particular components of a system, even when the models generally agree overall.

The effects of implemented process detail and model scope are usually most apparent under changing conditions (such as changing nutrient loads or fishing pressures). A change in conditions or pressures on a system may be beyond the "range of applicability" of an empirical model or may expose a flaw in a chosen formulation (Murray 2001, chapter5, chapter 6, chapter 7). I undertook many evaluations of different

aspects of model structure as part of an investigation of the effect of model structure on the behaviour of ecosystem models. It was repeatedly found that formulations of varying complexity can have very similar dynamics, or show only small divergences, under baseline conditions, but show much larger differences under altered nutrient loads or fishing pressures. For example, the problems associated with spatial resolution that are too restricted, or overly simplified trophic structures, or grazing and mortality terms that do not include some form of limitation all lead to poor performance under changing conditions. Thus, performance under changing conditions is an important measure of how robust model behaviour is to the level of complexity employed in a particular aspect of model structure or scope.

One of the clearest symptoms of this problem is model instability or manifestation of aberrant behaviours. This was one way to identify the potential weaknesses of the benthic deposit feeder group in BM2 (chapter 3). In certain circumstances the model allows this group to undergo almost exponential growth, an indication that this poorly known group has had a critical limiting factor omitted from the formulation during model development. While this highlights an area that needs more attention in the field, it is also an area that would have been missed if the model had been considered only under a restricted set of conditions.

Unfortunately, model failure need not be expressed in such an obvious way. A model that incorrectly specifies some process (like feeding or mortality) or has a scope that is too restricted may still appear to have "acceptable" behaviour (in relation to its state under current conditions), but the predicted behaviour may be incorrect (with regard to what would really occur) (chapters 4 – 6). For example, the lack of spatial structure in the 1 box model evaluated in Murray (2001) causes it to overestimate the nutrient loads that the Port Phillip Bay could tolerate (as predicted by the 59-box version) by 30%. This is a large problem if this version of the model is used to guide

management of nutrient loading and water quality in this bay.

8.6 Conclusions

The multitude of links and processes that make up a real ecosystem mean that the ultimate effects of anthropogenic actions will probably be much wider than expected and may even lead to counterintuitive outcomes. Ecosystem models are a prime candidate as a tool to aid in the understanding of these potential outcomes. This does not mean they do not have potential drawbacks (often to do with their own size and complexity), but careful consideration of these problems and the intelligent application of the models (particularly in a confirmatory framework) can avoid or minimise many of these problems. As concerns and management at a system level become an increasing focus of many sectors of human society, ecosystem models can be a valuable tool in addressing such issues (Walters et al. 1997). However, greater understanding of the effects of model structure and scope on model performance are necessary. This is particularly the case if we are to avoid the situation where frustration resulting from poorly structured ecosystem models, or the inappropriate use of existing ecosystem models, leads us to reject the modelling approach altogether.

Studies of the effect of model structure that have already taken place indicate that there is a humped form to the relationship between model detail and performance (Costanza and Sklar 1985, Håkanson 1995, this thesis). Too much complexity leads to too much uncertainty and problems to do with interpretation of the model's dynamics and predictions, while too little detail results in models that cannot produce realistic behaviours. These studies have also provided a few important guidelines which can usefully extend or augment the "rules of thumb" proposed in earlier works on ecological models (Wiegert 1977, O'Neill and Rust 1979, Cale and Odell 1980, Innis and Rextad 1983, Halfon 1983 a and b, Gardner et al. 1982, Iwasa et al. 1987):

(1) Physiological detail is not always necessary. However, the use of explicit physiological detail can be important in certain circumstances (such as oligotrophic conditions when simple assumptions about nutrient uptake and the ratio of limiting nutrients are violated).

(2) If an important process or linkage (e.g. to an external web) is poorly known, or is not explicitly represented in the model, then an empirical representation should be included in its place. This can avoid introducing uncertainty without risking the degradation of performance associated with neglecting a crucial aspect of a system.

(3) Some level of spatial resolution is likely to be necessary for adequate performance of the model. A 1-box model is unlikely to be sufficient, as space is itself an important system resource. This is particularly true in systems where benthic groups are important. Moreover, there must be enough spatial resolution in the model to capture the major physical characteristics of the system. Trophic self-simplification of the web (the loss of one or more components from the web) is often a good indicator of an overly restricted spatial representation.

(4) Sampling frequency (the time period at which model output is recorded) can have a large impact on model interpretation and the predictions deduced from the output. At a system level, a 2-4 weekly scheme is an adequate compromise between excessive noise and a loss of information.

(5) The inclusion of a complete trophic web at the level of species is neither necessary nor desirable, but the way in which the web is handled is critical. The use of functional groups is a successful means of representing the system web realistically (particularly if some age or size structure is included for the highest groups). Aggregation beyond the level of functional groups is ill advised, and omission of the least important groups is a better strategy if further simplification is necessary. Moreover, simplifying a model web (which represents the food web of an

entire system aggregated to the level of functional groups) to less than 20-25% of its original size is rarely beneficial, as representing the distinctions between large and small, or mobile and sedentary, groups may be crucial.

(6) Quadratic closure of the top-most parts of the trophic web is a successful method of closing the web, regardless of its size. The explicit inclusion of the highest predators may only be necessary when they are of direct interest.

(7) The form of the grazing functions used must be given careful consideration so that they contain enough flexibility without introducing extraneous detail. Holling "type-I" responses are unlikely to be sufficient (especially under changing conditions), but the more complex Holling type functions may be acceptable. More sophisticated responses, incorporating more behavioural dynamics (e.g. balancing predator avoidance with the need to forage) may be required in some circumstances, but the value of their inclusion should be checked.

In summary, potentially the best rule of thumb to remember is, in the words of Albrecht (1992), "as simple and as highly aggregated as possible and as complex and disaggregated as necessary!".

The topic of the effect of model complexity on model behaviour and performance is far from a closed chapter, especially with regard to ecosystem models. Within the context of trophic complexity and ECOSIM, Walters (pers. com.) stresses that "this [exploration of the effects] is a really crucial issue that has not yet been systematically explored by any of the science groups involved in ECOSIM modeling." However, this point is not restricted to trophic complexity or ECOSIM, but pertains to many facets of model structure and the many methodologies and ecosystem models currently in use. The work covered in this review is a useful start, but it is still early days.

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Appendix A: Biomass, production and consumption per set for real bays.

Values marked with the superscript ^{U} or ^{L} indicate bays that mark the bounds (upper and lower) of the range for that set in Figure 1.4.

Table A.1: Dissolved inorganic nitrogen (DIN), chlorophyll a (chl a) and primary production for real bays.

Country	Bay	DIN (mmol DIN m^{-3})	Chl a (mg chl a m^{-3})	Production (mg C m^{-2} d^{-1})	References
Australia	Albatross Bay	1.8	1.5		Burford et al. 1995
	Port Phillip Bay	0.8	1.0	364 - 574	Harris et al. 1996, Murray and Parslow 1997, Fulton and Smith in prep
Brazil	Baia de Guanabara	28.0	57.0		Kjerfve et al. 1997
	Patos Lagoon	5.6 - 9.2	2.3 - 11.3		Abreu et al. 1995
Canada	Bedford Basin	3.6 - 21.5	5.7 - 11.3		Monbet 1992
	St Lawerence Estuary			992	Tremblay et al. 1997
Chile	Strait of Magellan			218	Saggiomo et al. 1994
	Tongoy Bay			2110	Wolff 1994
France	Bay of Brest			1278	Del Amo et al. 1997
India	Cochin Backwater	5.7	6.1		Monbet 1992
Italy	Palude della Rosa			23	Carrer and Opitz 1999
Mexico	Bahia de Los Angeles	1.0 - 1.5	1.0^{L} - 7.0	800	Delgadillo-Hinojosa et al. 1997
	Tampamachoo Lagoon			300	Rosado-Solorzano and Guzmán del Próo 1998
	Terminos Lagoon			96	Manickchand-Heileman et al. 1998
Netherlands	Wadden Sea	3.9	7.7		Monbet 1992
New Zealand	Beatrix Bay	0.2^{L} - 1.4	2.0 - 4.1		Gibbs and Vant 1997
Philippines	Laguna de Bay			2681 - 6632	Delos Reyes and Martens 1994
Spain	Urdaibai Estuary			1415	Iriarte et al. 1996
South Africa	Kromme Estuary			49	Heymans and Baird 1995
South Orkney	Signy Island			72 - 188	Clarke and Leakey 1996
UK	Firth of Clyde	7.0 - 9.4	2.0 - 6.3		Monbet 1992, Bock et al. 1999
USA	Apalachicola Bay	2.2 - 5.0	5.4 - 7.1	750	Monbet 1992, Mortazavi et al. 2000
	Buzzards Bay	4.2	8.7		Borkman and Turner 1993

Table A.1: Continued.

Country	Bay	DIN (mmol DIN m^{-3})	Chl a (mg chl a m^{-3})	Production (mg C m^{-2} d^{-1})	References
	Charlotte Harbour	6.6 - 15.3	4.8 - 15.2		Monbet 1992
	Chesapeake Bay	5.5 - 42.2	9.9 - 33.7		Monbet 1992
	Chincoteague Bay	7.5	22.0	1100	Boynton et al. 1996
	Columbia River	15.3	7.3		Monbet 1992
	Flax Pond	4.6 - 5.2	5.5 - 5.8		Monbet 1992
	Galveston Bay	16.0	6.9		Santschi 1995
	Hilsborough	47.1 - 48.1	13.4 - 19.3		Monbet 1992
	Hudson River	33.6 - 45.6	2.7 - 23.7		Monbet 1992
	Isle of Wight Bay	11.0	38.0		Boynton et al. 1996
	James River	54.3	41.4		Monbet 1992
	Long Island Sound	8.2	8.6		Borkman and Turner 1993
	Massachusetts Bay	6.5	3.1		Borkman and Turner 1993
	Monterey Bay	5.0 - 10.0	3.0 - 6.0		Pennington and Chavez 2000
	Narragansett Bay	4.7 - 10.2	9.1 - 10.3		Monbet 1992, Smayda 1983
	Neuse River	5.0	12.8		Monbet 1992
	North Inlet	27.0	7.0		Monbet 1992
	Patuxent River	8.6 - 63.9	12.3 - 48.1		Monbet 1992
	Peconic Bay	2.6	2.9		Turner et al. 1983
	Potomac River	8.8 - 119.2[U]	12.7 - 78.9		Monbet 1992
	Rappahanock River	3.4 - 24.7	4.5 - 21.7		Monbet 1992
	Rhode River	10.0 - 15.3	8.1 - 150.0[U]		Monbet 1992, Gallegos et al. 1997
	San Francisco Bay	4.0 - 40.9	8.9 - 25.2		Monbet 1992
	South River	9.7	16.8		Monbet 1992
	York River	4.8 - 4.9	3.3 - 4.0		Monbet 1992

Table A.2: Zooplankton biomass, production and consumption for real bays.

Country	Bay	Zooplankton (mg AFDW m^{-3})	Production (mg C m^{-2} d^{-1})	Consumption (mg C m^{-2} d^{-1})	References
Australia	Port Phillip Bay	68.4 - 68.5	143.4 - 169.0	232.7	Holloway and Jenkins 1993, Beattie et al. 1996, Murray and Parslow 1997, Fulton and Smith in prep
Baltic	Northern Baltic		32.9		Koski et al. 1999
Chile	Tongoy Bay	20.0	197.3	867.9	Wolff 1994
Denmark	Kattegatt	106.0	400.0		Kiørboe and Nielsen 1994a, b
France	Arcachon Bay	150.0			Poulet et al. 1996
	Cantabrian Coast	82.4 - 102.0			Poulet et al. 1996
	Gironde	43.8			Plounevez and Champalbert 1999
	Ushant	50.0			Poulet et al. 1996
	West English Channel	150.0			Poulet et al. 1996
France/UK	Celtic Sea	200.0			Poulet et al. 1996
Finland	Bothnian Bay		16.4		Koski et al. 1999
	Sällvik		28.8		Koski et al. 1999
	Storfjärden		31.0		Koski et al. 1999
	Längden		76.9		Koski et al. 1999
India	Bay of Bengal	36.3			Kumari and Goswami 1993
	Goa		48.9		Goswami and Padmavati 1996
Ireland	West Irish Sea	26.9			Dickey-Collas et al. 1996
Italy	Palude della Rosa	72.7	18.1		Carrer and Opitz 1999
Jamaica	Kingston Harbour	331.0			Hopcroft et al. 1998
Mexico	Chetumal Bay	10.7^{L}			Gasca and Castellanos 1993
	Terminos Lagoon	322.0	26.3	111.1	Manickchand-Heileman et al. 1998
	Tampamachoo Lagoon	79.2	4.4	22.2	Rosado-Solorzano and Guzmán del Próo 1998
Netherlands	Westerschelde	60.0			Soetaert and Herman 1994
Philippines	Laguna de Bay	$400.0 - 563.0^{U}$	253.2 - 456.9	1019.8 - 1823.3	Delos Reyes and Martens 1994
Russia	Barents Sea	60.0			Sakshaug et al. 1994
South Africa	Kromme Estuary	30.0	11.2	36.5	Heymans and Baird 1995
Spain	Galicia	125.0			Poulet et al. 1996
	La Coruna	170.8			Poulet et al. 1996

Table A.2: Continued.

Country	Bay	Zooplankton (mg AFDW m^{-3})	Production (mg C m^{-2} d^{-1})	Consumption (mg C m^{-2} d^{-1})	References
Sweden	Central Baltic		16.4		Koski et al. 1999
Taiwan	Chiku Lagoon	40.8			Lin et al. 1999
UK	Plymouth	30.0			Harvey 1950
USA	Chesapeake Bay	71.4 - 148.0			Park and Marshal 2000
	Corpus Christi Bay	144.8			Buskey 1994
	Monterey Bay	28.0			Olivieri and Chavez 2000
	Narragansett Bay	201.8			Durbin and Durbin 1998

Table A.3: Fish biomass, production and consumption for real bays.

Country	Bay	Total fish (g AFDW m^{-2})	Total production (mg AFDW m^{-2} d^{-1})	Total consumption (mg AFDW m^{-2} d^{-1})	References
Australia	Albatross Bay	5.5			Blaber et al. 1994
	Alligator Creek	2.4			Robertson and Duke 1990
	Bagot Point		65.2		Edgar and Shaw 1995
	Barker Inlet		82.2		Edgar and Shaw 1995
	Botany Bay	1.4			Bell et al. 1984
	Cararma Inlet		14.6		Edgar and Shaw 1995
	Cloudy Lagoon		69.8		Edgar and Shaw 1995
	Crib Point		13.1		Robertson 1980
	Embley Estuary	15.8			Blaber et al. 1989
	French Island		3.6		Edgar and Shaw 1995
	Frenchmans Bay		5.5		Edgar and Shaw 1995
	Groote Eylandt	5.5			Blaber et al. 1994
	Great Barrier Reef	35.6			Williams and Hatcher 1983
	Gulf of Carpentaria	2.7			Blaber et al. 1994
	Lake King		58.6		Edgar and Shaw 1995
	Moreton Bay	3.1			Morton 1990
	North West Shelf	> 0.47			Sainsbury 1987

Table A.3: Continued.

Country	Bay	Total fish (g AFDW m^{-2})	Total production (mg AFDW m^{-2} d^{-1})	Total consumption (mg AFDW m^{-2} d^{-1})	References
	One Tree	47.6[U]			Russell 1977
	Parker Point		44.2		Edgar and Shaw 1995
	Peel-Harvey Estuary	0.5[L]			Loneragan et al. 1986
	Porpoise Bay		2.0		Edgar and Shaw 1995
	Port Gawler		12.8		Edgar and Shaw 1995
	Port Phillip Bay	3.3	6.2	55.7 - 72.2	Hall 1992, Parry et al. 1995, Fulton and Smith in prep
	Princess Royal Bay		90.9		Edgar and Shaw 1995
	Rockingham		36.2		Edgar and Shaw 1995
	South East Gulf	2.8			Blaber et al. 1994
	Thomsons Bay		1.6		Edgar and Shaw 1995
	Western Port Bay	1.2			Robertson 1980
	Woodmans Point		5.2		Edgar and Shaw 1995
Bermuda	Bermuda	10.8			Bardach 1959
Chile	Tongoy Bay	4.6	54.6	377.3	Wolff 1994
China	Western Yellow Sea	>0.1			Rhodes 1998
Crete	Heraklion Bay	9.5			Kallianiotis et al. 2000
Egypt	Gulf of Aqaba	21.2			Whitfield 1993
Eritrea	Dahlak Archipelago	7.7			Russell 1977
France	Port Cros	1.7			Francour 1997
Hawaii	French Frigate Shoals	29.7			Freidlander and Parrish 1997
	Hanalei Bay	16.6			Freidlander and Parrish 1997
	Hawaii	20.4			Russell 1977
	Hulopoe-Manele	44.6			Freidlander and Parrish 1997
	Kaneohe Bay	23.8			Freidlander and Parrish 1997
	Midway Atoll	28.6			Freidlander and Parrish 1997
	Oahu	20.5 - 21.0			Freidlander and Parrish 1997
	Waikiki	5.8			Freidlander and Parrish 1997
India	Marmugao Bay	1.5			Ansari et al. 1995
	Aguada Bay	1.1			Ansari et al. 1995

Table A.3: Continued.

Country	Bay	Total fish (g AFDW m^{-2})	Total production (mg AFDW m^{-2} d^{-1})	Total consumption (mg AFDW m^{-2} d^{-1})	References
Indian Ocean	Mayotte	30.9			Letourneur et al. 2000
	Réunion	21.45			Letourneur 1998
Italy	Palude della Rosa	2.5		10.5	Carrer and Opitz 1999
Mexico	Huizache-Caimanero Lagoon	2.3	16.0		Warburton 1979
	Tampamachoo Lagoon	1.2	5.7	63.3	Rosado-Solorzano and Guzmán del Próo 1998
	Teacapan-Agua Brava Lagoon	2.2			Flores-Verdugo et al. 1990
	Terminos Lagoon	1.4 - 2.5	4.0	61.5	Manickchand-Heileman et al. 1998
New Caledonia	Barrier reefs	> 5.07			Letourneur et al. 2000, Kulbicki et al. 2000
	Belep Island	23.1			Letourneur et al. 2000
	Chesterfield Islands	30.8			Letourneur et al. 2000
	Cooks Reef	39.0			Letourneur et al. 2000
	East Reefs	15.8			Letourneur et al. 2000, Kulbicki et al. 2000
	Francais Reef	44.7			Letourneur et al. 2000
	Fringing reefs	> 4.99			Letourneur et al. 2000, Kulbicki et al. 2000
	Intermediate reefs	> 5.87			Letourneur et al. 2000, Kulbicki et al. 2000
	Lagoon bottoms	> 8.41			Kulbicki et al. 2000
	North Lagoon	2.0			Wantiez 1998
	Ouvéa	49.2			Letourneur et al. 2000
	South Reefs	25.9			Letourneur et al. 2000
	St Vincent Bay	> 1.07 - > 1.89			Wantiez 1996, Wanteiz et al. 1996
	West Reefs	25.8			Letourneur et al. 2000, Kulbicki et al. 2000
New Zealand	Goat Island	11.4			Russell 1977
Pacific Ocean	Eniwetok Atoll	10.6			Odum and Odum 1955
Philippines	Laguna de Bay	3.2 - 4.2	37.2 - 50.4	78.0 - 299.4	Delos Reyes and Martens 1994
Russia	Barents Sea	7.9			Sakshaug et al. 1994

Table A.3: Continued.

Country	Bay	Total fish (g AFDW m^{-2})	Total production (mg AFDW m^{-2} d^{-1})	Total consumption (mg AFDW m^{-2} d^{-1})	References
Solomon Islands	Solomon Islands	2.6			Blaber and Milton 1990
South Africa	Cape of Good Hope	10.9			Whitfield 1993
	Kromme Estuary	12.4	11.9	171.3	Heymans and Baird 1995
	Durban	15.1			Berry et al. 1982
	Swartvlei Lake	2.7			Whitfield 1993
Spain/France	North West Mediterranean	15.0			McClanahan and Sala 1997
Taiwan	Chiku Lagoon	47.6			Lin et al. 1999
Thailand	Sichang Islands	18.3			Menasveta et al. 1986
	South China Sea	> 1.0			Wanteiz et al. 1996
UK	Ardmucknish Bay	>0.88			Gibson et al. 1993
	Plymouth	2.9			Harvey 1950
USA	Bathtub Rock	15.1			Quast 1968
	Biscayne Bay	0.7			Brock 1977
	Bogue Sound	1.3			Adams 1976
	Chesapeake Bay	1.2 - 12.0	7.1		Lubbers et al. 1990
	Corpus Christi	4.9			Whitfield 1993
	Del Mar	8.3			Quast 1968
	Horn Island	1.6			Ross et al. 1987
	Laguna Madre	2.6			Whitfield 1993
	Monterey Bay	12.4			Russell 1977
	Mustang Island	1.6 - 1.65			Russell 1977
	Papalote Bay	7.6			Quast 1968
	Santa Barbara Channel	25.5			Love et al. 2000
	St Andrew Bay	0.6			Whitfield 1993
	Sth New England	2.0			Russell 1977
	Whitewater Bay	2.5			Thayer et al. 1987
USA (Alaska)	Prince William Sound	1.5			Dean et al. 2000
Virgin Islands	Virgin Islands	35.2			Russell 1977

Table A.4: Biomass of benthos and meiobenthos, maximum water depth, and total benthic production and consumption for real bays.

Country	Bay	Total benthos > 1mm (g AFDW m^{-2})	Meiobenthos (g AFDW m^{-2})	Maximum depth (m)	Total production (mg AFDW m^{-2} d^{-1})	Total consumption (mg AFDW m^{-2} d^{-1})	References
Australia	Bagot Point	11.4			142.0		Edgar and Shaw 1995
	Barker Inlet	58.0			524.0		Edgar and Shaw 1995
	Cararma Inlet	6.3			65.7		Edgar and Shaw 1995
	Cloudy Lagoon	7.9			94.5		Edgar and Shaw 1995
	Crib Point	7.3			92.5		Edgar and Shaw 1995
	French Island	8.0			115.0		Edgar and Shaw 1995
	Frenchmans Bay	6.0			61.0		Edgar and Shaw 1995
	Lake King	40.0			566.5		Edgar and Shaw 1995
	Parker Point	1.0^{L}			18.0		Edgar and Shaw 1995
	Porpoise Bay	10.3			132.0		Edgar and Shaw 1995
	Port Gawler	76.0			516.5		Edgar and Shaw 1995
	Port Phillip Bay	26.4 - 33.5	0.2	24	178.0 - 424.0	580.9 - 1466.0	Poore 1992, Wilson et al. 1993, Wilson et al. 1998, Harris et al. 1996, Fulton and Smith in prep
	Princess Royal Bay	17.3			215.7		Edgar and Shaw 1995
	Rockingham	14.5			204.5		Edgar and Shaw 1995
	Seven Mile Beach				31.35		Edgar 1990
	Thomsons Bay	5.4			64.3		Edgar and Shaw 1995
	Western Port Bay	17.3			126.2		Robertson 1984, Edgar et al. 1994
	Woodmans Point	2.4			38.9		Edgar and Shaw 1995
Bermuda	Castle Harbour		1.0	13			Rudnik et al. 1985
Canada	Flemish Cap	2.5					Steimle 1985
	Georges Bank	27.4					Steimle 1985
	Grand Banks	4.6					Steimle 1985
	Labrador	2.2					Steimle 1985
	Nain Bay	45.8					Mills 1975
	Newfoundland	6.5					Steimle 1985
	North Nova Scotia	17.5					Steimle 1985
	Scotian Shelf	2.3			416.5		Steimle 1985

Table A.4: Continued.

Country	Bay	Total benthos > 1mm (g AFDW m^{-2})	Meiobenthos (g AFDW m^{-2})	Maximum depth (m)	Total production (mg AFDW m^{-2} d^{-1})	Total consumption (mg AFDW m^{-2} d^{-1})	References
Chile	Tongoy Bay	16.3	1.8	90	158.2	685.1	Wolff 1994
Denmark	Kysing Fjord		0.2	1			Rudnik et al. 1985
	Oresund		2.5	54			Rudnik et al. 1985
France	Arcachon Bay	5.4					Bachelet et al. 1996
	Bay of Banyuls-sur-mer	3.3 - 4.3	87.0	1.3			Rudnik et al. 1985, Grémare et al. 1998
	Bay of Brest	19.2					Jean and Thouzeau 1995
	Bay of Lyon		0.4	30			Rudnik et al. 1985
	Etang de Thau Lagoon	43.0					Palomares et al. 1993
	Gironde Estuary		0.4	5			Santos et al. 1996
France/Spain	North West Mediterranean	70.7					McClanahan and Sala 1997
Finland	Tvarminne		1.5	55			Rudnik et al. 1985
Germany	Helgoland Bight		0.4	49			Rudnik et al. 1985
	Kiel Bight		0.2	26			Rudnik et al. 1985
India	Bay of Bengal		$<0.1^{L}$	230			Rudnik et al. 1985
	Goa		0.2	30			Rudnik et al. 1985
Ireland	Irish Sea		0.5	121			Rudnik et al. 1985
Iran/Iraq	Tigris and Euphrates Estuary		0.2	18			Rudnik et al. 1985
Italy	Adriatic Sea		0.2	17			Rudnik et al. 1985
	Palude della Rosa	96.7	10.2^{U}	0.5		230.2	Carrer and Opitz 1999
Mexico	Celestun Lagoon	2.6	3.3				Chavez et al. 1993
	Gulf of Mexico	115.0					Talley et al. 2000
	Tampamachoo Lagoon	2.0	1.2		54.2	236.8	Rosado-Solorzano and Guzmán del Próo 1998
	Terminos Lagoon	14.6	5.2	3.5	316.4	1446.8	Manickchand-Heileman et al. 1998
Netherlands	Dutch Wadden Sea	16.5					Möller et al. 1985
	Grevelingen Estuary				147.9		Steimle 1985
	North Wadden Sea				137.0		Steimle 1985
	Wadden Sea				71.2		Steimle 1985

Table A.4: Continued.

Country	Bay	Total benthos > 1mm (g AFDW m^{-2})	Meiobenthos (g AFDW m^{-2})	Maximum depth (m)	Total production (mg AFDW m^{-2} d^{-1})	Total consumption (mg AFDW m^{-2} d^{-1})	References
	Westerschelde		0.3	20			Soetaert et al. 1994
North Sea	Fladen		0.5	101			Rudnik et al. 1985
Pacific	Eniwetok Atoll	92.0					Odum and Odum 1955
Philippines	Laguna de Bay	5.6			136.0 - 155.0	544.2 - 628.5	Delos Reyes and Martens 1994
Poland	Gulf of Gadansk	33.3					Drgas et al. 1998
South Africa	Kromme Estuary	30.5	0.4	3	183.4	5292.2	Heymans and Baird 1995
South Orkney	Signy Island		4.5	10			Vanhove et al. 1998
Spain	Bay of Cadiz	18.4			61.2		Arias and Drake 1994
	Ria de Arosa		0.2	19			Rudnik et al. 1985
	Ria de Muros		<0.1	22			Rudnik et al. 1985
Sweden	Baltic Sea	21.0			2.1		Möller et al. 1985
	Bassholm	5.6			67.8		Möller and Rosenberg 1982
	Bothnian Bay		0.3	220			Rudnik et al. 1985
	Bothnian Sea	12.8	0.7	100	1.2		Möller et al. 1985, Rudnik et al. 1985
	Central Baltic		1.2	46			Rudnik et al. 1985
	Gota Estuary		0.2	52			Rudnik et al. 1985
	Gullmarsvik	2.4			14.9		Möller and Rosenberg 1982
	Kungsbacha		0.1	16			Rudnik et al. 1985
	Mid-Baltic				29.6		Steimle 1985
	Northern Baltic				19.7		Steimle 1985
	Sandvik	1.6			13.0		Möller and Rosenberg 1982
	Skagerrak	38.0			416.5		Möller et al. 1985
	Swedish Sound	5.2			36.8		Möller et al. 1985
	Sweden	25.4					Pihl-Baden and Pihl 1984
	West Central Baltic		0.1	211			Rudnik et al. 1985
Taiwan	Chiku Lagoon	59.0					Lin et al. 1999
UK	Clyde Sea		0.2	166			Rudnik et al. 1985
	Cornwall				36.4		Steimle 1985
	English Channel		0.2	45			Rudnik et al. 1985
	Hamble Spit				602.7		Hibbert 1976
	Liverpool Bay		0.5	10			Rudnik et al. 1985

Table A.4: Continued.

Country	Bay	Total benthos > 1mm (g AFDW m^{-2})	Meiobenthos (g AFDW m^{-2})	Maximum depth (m)	Total production (mg AFDW m^{-2} d^{-1})	Total consumption (mg AFDW m^{-2} d^{-1})	References
	Loch Nevis		0.7	146			Rudnik et al. 1985
	Lynher Estuary	13.3			36.5		Warwick and Price 1975
	Northumberland Coast		0.3	80			Rudnik et al. 1985
	Plymouth	17.0					Harvey 1950
	Scotland	11.2					Hibbert 1976
	Southhampton	166.0[U]					Hibbert 1976
	Tamar Estuary				36.2		Steimle 1985
	Ythan Estuary				294.2		Steimle 1985
USA	Biscayne Bay	6.4					Brock 1977
	Block Island Sound	15.8					Steimle 1982
	Buzzards Bay		0.3	18			Rudnik et al. 1985
	Cape Cod Bay		1.0	41			Rudnik et al. 1985
	Chesapeake Bay	5.0 - 50.0			29.3 - 330.1		Fredette et al. 1990, Dauer and Alden 1995
	Chesapeake Bight	10.1					Steimle 1985
	Christiansem Basin	19.1 - 23.6					Steimle 1985
	Delaware Bay				145.2		Steimle 1985
	Long Island Sound		0.6	30	64.7		Rudnik et al. 1985, Vanhove et al. 1998
	Martha's Vineyard Sound		0.2	99			Rudnik et al. 1985
	Massachusetts	24.6					Steimle 1985
	Narrangansett Bay		2.9	7			Rudnik et al. 1985
	Nauset Marsh	47.7			73.6		Heck et al. 1995
	New Jersey Shelf	28.0					Steimle 1985
	New York Bight	7.3 - 25.1	0.4	24	130.4		Steimle 1985, Rudnik et al. 1985
	Niantic River		4.5	1			Rudnik et al. 1985
	San Francisco Bay	13.3					Heck et al. 1995
	South Carolina		1.3	1			Rudnik et al. 1985
	St Joseph Bay	67.5			702.1		Valentine and Heck 1993

Table A.5: Macrophyte biomass and primary production for real bays.

Country	Bay	Total macrophytes (g AFDW m^{-2})	Total production (mg AFDW m^{-2} d^{-1})	References
Australia	Port Phillip Bay	1.4 – 15.1	53.9 - 174.9	Chidgey and Edmunds 1997, Murray and Parslow 1997, Fulton and Smith in prep
	Western Port Bay	167.0		Robertson 1980
Chile	Tongoy Bay	5.5	2.8	Wolff 1994
France	Etang de Thau Lagoon	94.2		Gerbal and Verlaque 1995
France/Spain	North West Mediterranean	199.5		McClanahan and Sala 1997
Italy	Palude della Rosa	168.0	785.8	Carrer and Opitz 1999
Mexico	Celestun Lagoon	35.0		Chavez et al. 1993
	Tampamachoo Lagoon	10.5	168.9	Rosado-Solorzano and Guzmán del Próo 1998
	Terminos Lagoon	239.0	3449.0	Manickchand-Heileman et al. 1998
New Zealand	Otago Harbour	141.2		Grove and Probert 1999
Pacific Ocean	Eniwetok Atoll	618.2^{U}		Odum and Odum 1955
Philippines	Laguna de Bay	1.1^{L}	33.5	Delos Reyes and Martens 1994
South Africa	Kromme Estuary	147.9	5255	Heymans and Baird 1995
Sweden	Gota River Bays	591.3		Pihl et al. 1994
USA	Chesapeake Bay	33.1 - 46.6	831.5	Murray and Wetzel 1987, Madden and Kemp 1996, Buzzelli et al. 1998
	Childs River	193.6		Valiela et al. 1992
	Bass Harbour Marsh	64.6 - 183.5		Kinney and Roman 1998
	Branford River	81.4		Welsh 1980
	Green Hill Pond	164.4		Kinney and Roman 1998
	Mumford Cove	204.2		Kinney and Roman 1998
	Ninigret Pond	141.2		Kinney and Roman 1998
	Quashnet River	74.8		Valiela et al. 1992
	Sage Lot Pond	31.7		Valiela et al. 1992
	Waquoit Bay	71.6		Valiela et al. 1997

Table A.6: Total detritus for real bays.

Country	Bay	Total detritus (g AFDW m^{-2})	References
Australia	Bagot Point	3.2^{L}	Edgar and Shaw 1995
	Cararma Inlet	10.6	Edgar and Shaw 1995
	Lake King	101.0	Edgar and Shaw 1995
	Porpoise Bay	4519.0	Edgar and Shaw 1995
	Port Gawler	331.0	Edgar and Shaw 1995
	Port Phillip Bay	1731.0 - 2953.4	Nicholson et al. 1996, Fulton and Smith in prep
	Rockingham	1659.0	Edgar and Shaw 1995
	Woodmans Point	1940.0	Edgar and Shaw 1995
French Polynesia	Tiahura	677.5	Ariasgonzalez et al. 1998
Italy	Palude della Rosa	750.4	Carrer and Opitz 1999
Mexico	Terminos Lagoon	12.7	Manickchand-Heileman et al. 1998
South Africa	Kromme Estuary	3000.0	Heymans and Baird 1995
Taiwan	Chiku Lagoon	48.6	Lin et al. 1999
USA	Chesapeake Bay	10417.0^{U}	Roden and Tuttle 1996

Table A.7: Biomass and primary production of microphytobenthos for real bays.

Country	Bay	Microphytobenthos (mg chl a m^{-2})	Production (mg C m^{-2} d^{-1})	References
Australia	Peel-Harvey Estuary	295.0^{U}		MacIntyre et al. 1996
	Port Phillip Bay	25.0 - 51.7	101.1 - 240.5	Murray and Parslow 1997, Fulton and Smith in prep
Canada	Bay of Fundy	255.0		Hargrave et al. 1983
Denmark	Danish Fjords		318.0	Grøntved 1960
	Smalandshavet		555.0	MacIntyre et al. 1996
France	Golfe de Fos	38.0		MacIntyre et al. 1996
	Mediterranean Coast	44.0		Schreiber and Pennock 1995

Table A.7: Continued.

Country	Bay	Microphytobenthos (mg chl a m^{-2})	Production (mg C m^{-2} d^{-1})	References
Madagascar	Madagascar	58.0	181.0	Schreiber and Pennock 1995
Netherlands	Dutch Wadden Sea	220.0 - 225.0	485.0 - 567.5	Cadée and Hegeman 1977, MacIntyre et al. 1996
	Ems-Dollard Estuary	65.0 - 282.5	463.0 - 985.0	Colijn and de Jonge 1984, MacIntyre et al. 1996
	Lake Grevelingen	215.0	295.0	MacIntyre et al. 1996
Russia	Vostok Bay	135.0		MacIntyre et al. 1996
Slovenia	Bay of Prian		240.0	MacIntyre et al. 1996
South Africa	Kromme Estuary	1.6^{L}	232.0	Heymans and Baird 1995
Spain	Ria de Arosa	66.5		MacIntyre et al. 1996
Sweden	Laholm Bay	24.5	147.0	MacIntyre et al. 1996
	Oresund	75.5	565.0	Schreiber and Pennock 1995
UK	Loch Ewe		17.8	Steele and Baird 1968
	Ythan estuary		84.9 - 117.5	Leach 1970
USA	Bolsa Bay	285.0	494.5	Schreiber and Pennock 1995
	Boston Harbour	190.0		MacIntyre et al. 1996
	Buzzards Bay	52.5		MacIntyre et al. 1996
	Chesapeake Bay	35.0		MacIntyre et al. 1996
	Chukchi Sea	73.5 - 180.0	13.7	Matheke and Horner 1974, MacIntyre et al. 1996
	Delaware Estuary	122.5		MacIntyre et al. 1996
	Duplin River Marsh		289.0	MacIntyre et al. 1996
	Graveline Bay	215.0		MacIntyre et al. 1996
	La Jolla		182.5	MacIntyre et al. 1996
	Long Island Sound	113.5		MacIntyre et al. 1996
	Netarts Bay	162.5		MacIntyre et al. 1996
	North Inlet	65.0 - 70.0		MacIntyre et al. 1996
	Potter Pond Lagoon	235.0		MacIntyre et al. 1996
	San Antonio Bay	8.0 - 29.5	43.5	MacIntyre et al. 1996
	Tijuana Estuary		1472.0	MacIntyre et al. 1996
	Weeks Bay	15.6	246.6	Schreiber and Pennock 1995

Appendix B: Meaning of the acronyms, functional group codes and symbols used.

Table B.1: List of the acronyms commonly used in this thesis

Acronym	Meaning
BM2	Bay Model 2
CM	Model runs with nutrient loadings scaled to match the loadings of Chesapeake Bay
IGBEM	Integrated Generic Bay Ecosystem Model
PPB	Port Phillip Bay (near Melbourne, Australia)
PPBIM	Port Phillip Bay Integrated Model
PM	Model runs with nutrient loadings scaled to match the loadings of Port Phillip Bay

Table B.2: List of components in Bay Model 2 (BM2) and the Integrated Generic Bay Ecosystem Model (IGBEM), compared to those in the Port Phillip Bay Integrated Model (PPBIM). All living and dead components have nitrogen pools, in IGBEM they also have carbon and phosphorous pools.

		Model	
Component	Codename	BM2 / IGBEM	PPBIM
Diatoms*	PL	Y	Y
Autotrophic Flagellates	AF	Y	
Picophytoplankton	PS	Y	Y
Dinoflagellates	DF	Y	Y
Free-living Pelagic Bacteria	PFB	Y	
Pelagic Attached Bacteria**	PAB	Y	
Heterotrophic Flagellates	HF	Y	
Microzooplankton	ZS	Y	Y
Large Omnivorous Zooplankton	ZL	Y	
Large Carnivorous Zooplankton	ZLC	Y	Y
Planktivorous Fish	FP	Y	
Piscivorous Fish	FV	Y	
Demersal Fish	FD	Y	
Demersal Herbivorous Fish	FG	Y	
Macroalgae	MA	Y	Y
Seagrass	SG	Y	Y
Microphytobenthos*	MB	Y	Y
Macrozoobenthos (Epifaunal carnivores)	MZ	Y	
Benthic (Epifaunal) Grazers	BG	Y	
Benthic Suspension Feeders	BF	Y	Y
Infaunal Carnivores	BC	Y	
Benthic Deposit Feeders	BD	Y	
Meiobenthos	OB	Y	
Aerobic Bacteria	AEB	Y	
Anaerobic Bacteria	ANB	Y	
Labile Detritus	DL	Y	Y
Refractory Detritus*	DR	Y	Y
DON	DON	Y	Y
Ammonia	NH	Y	Y
Nitrate	NO	Y	Y
Dissolved Silicate	Si	Y	Y
Dissolved Oxygen	O2	Y	Y***
Light	IRR	Y	Y
Salinity	SAL	Y	Y
Sediment Grain Types	PHI	Y	Y
Bottom Stress	STRESS	Y	Y
Porosity	POR	Y	Y
Volume	VOL	Y	Y

* Also have an internal silicon pool.

** Only present as a separate entity in BM2, in IGBEM there is a single pelagic bacteria component.

*** Handled as nitrogen fluxes scaled by the Redfield ratio N:O = 1:16

Table B.3: List of main terms used in the equations in the appendices C to F. All terms, variables, constants and expressions are defined in the relevant appendices, but this table may be a useful quick reference for the main terms and conventions.

Term	Meaning
E	Excretion (ammonia produced by a consumer)
F	Fishing (catch)
G	Growth
M	Mortality
P	Uptake
R	Remineralisation
S	Sediment chemistry (nitrification or denitrification, the subscript will denote which on a case-by-case basis)
W	Waste (detritus produced by a consumer)
XX	All doubles (and triples) refer to components of the model (see Table A3 for definitions). They do not represent multiplications at any time and any multiplications will be explicitly denoted by a "·".

Appendix C: Rate of change and process equations for Bay Model 2

Note: For quick reference, a list of the main terms used in the equations in this appendix is given in Appendix B, Table B.3.

C.1 Rate of change equations

Autotrophs

Rate of change for standard water column primary producer (PX):

$$\frac{d(PX_w)}{dt} = G_{PX_w} - M_{lys,PX_w} - \sum_{\substack{i=\text{predator} \\ \text{groups}}} P_{PX_w,i} \quad \text{(C.1)}$$

$$\frac{d(PX_{sed})}{dt} = -M_{nat,PX_{sed}} \quad \text{(C.2)}$$

Where G_{PX} stands for the growth of PX, $M_{lys,PX}$ is the loss of PX due to lysis, $M_{nat,PX}$ is the natural mortality losses of PX when in the sediments and $P_{PX,I}$ are the losses of PX due to predation. The equations for the benthic primary producers are slightly different. The rate of change of microphytobenthos is given by:

$$\frac{d(MB_w)}{dt} = G_{MB_w} - M_{lys,MB_w} - \sum_{\substack{i=\text{water predator} \\ \text{groups}}} P_{MB_w,i} \quad \text{(C.3)}$$

$$\frac{d(MB_{sed})}{dt} = G_{MB_{sed}} - M_{nat,MB_{sed}} - \sum_{\substack{i=\text{sed predator} \\ \text{groups}}} P_{MB_{sed},i} \quad \text{(C.4)}$$

The macrophytes (MX) are restricted to the epibenthic layer and have no water column or sediment pools. The general form of their rate of change is as follows:

$$\frac{d(MX)}{dt} = G_{MX} - M_{MX} - \sum_{\substack{i=\text{predator} \\ \text{groups}}} P_{MX,i} \quad \text{(C.5)}$$

The process equations for primary producers are outlined below and modifications to these equations due to mixotrophy in dinoflagellates are noted in the main text of chapter 2.

Invertebrate Consumers

Rate of change for a standard invertebrate consumer (CX):

$$\frac{d(CX)}{dt} = G_{CX} - M_{CX} - \sum_{\substack{i=\text{predator} \\ \text{groups}}} P_{CX,i} - F_{CX} \qquad \text{(C.6)}$$

where F_{CX} stands for losses due to fishing on this group (this is set to zero in all standard runs of Bay Model 2 (BM2)). Invertebrate consumers are restricted to having only a water column or epibenthic or sediment pool and can not have pools in multiple layers.

Fish consumers

The following are the rates of change for a fish group (FX).

$$\frac{d(FX_{i,s})}{dt} = G_{FX_{i,s}} \qquad \text{(C.7)}$$

$$\frac{d(FX_{i,r})}{dt} = G_{FX_{i,r}} \qquad \text{(C.8)}$$

$$\frac{d(FX_{i,d})}{dt} = T_{IMM,FX_i} - T_{EM,FX_i} - M_{FX_i} - \sum_{\substack{j=\text{predator} \\ \text{groups}}} P_{FX,j} - F_{FX_i} \qquad \text{(C.9)}$$

Where the subscript i represents age group i (there is one equation for each age class included), s stands for structural weight (skeletal and other material that can not be reabsorbed), r for reserve weight (fats and other tissues that can be broken down when food is scarce) and d for density. The T terms represent the movement of fish in to ($T_{IMM,Fxi}$) and out of ($T_{EM,Fxi}$) the cell. In addition there are short-term spawning and recruitment events which effect the various FX pools. At the same point each year (the exact day dependent on the fish and with a window of +/- 14 days) the fish spawn and the materials required to do this is removed from the reserve weight of FX. At this point all fish are aged one age class and the oldest age class leaves the bay (this is used in place of a plus group as it is more representative of the dynamics of Port Phillip Bay

(Gunthorpe et al. 1997)). Sometime later (the exact period dependent on the group) the recruits settle out and their weights and density are assigned to the youngest age class.

The amount of reserve weight (mg N per individual) that is used up during spawning is given by

$$s_{FX_i} = \begin{cases} U_{FX_i} \cdot \max\left(0, \left(Z_{FX} \cdot \left(1+X_{RS}\right) \cdot FX_{i,s} - Y_{FX}\right)\right) & , \; FX_{i,s} + FX_{i,r} > \left(1+X_{RS}\right) \cdot FX_{i,s} \\ U_{FX_i} \cdot \max\left(0, \left[\begin{array}{c} Z_{FX}\left(1+X_{RS}\right) \cdot FX_{i,s} + \left(FX_{i,s} + FX_{i,r}\right) \\ -Y_{FX} - \left(1+X_{RS}\right) \cdot FX_{i,s} \end{array}\right]\right) & , \; FX_{i,s} + FX_{i,r} < \left(1+X_{RS}\right) \cdot FX_{i,s} \end{cases} \quad \text{(C.10)}$$

where U_{Fxi} is the proportion of age group i that is reproductively mature, Z_{FX} is the fraction of the weight of FX used in spawning, Y_{FX} is the spawning function constant and X_{RS} is the ratio of structural to reserve weight in well fed fish.

The formulations for recruitment are given in the main text of chapter 2 and Table 2.2. It should be noted that the biomass of larvae of fish group FX in cell j at time t (L_{tj}), referred to in Table 2, is determined as follows:

$$L_{tj} = \sum_{i=\text{age class}} s_{FX_i} \cdot FX_{i,d} \quad \text{(C.11)}$$

Inanimate pools

Rates of change for ammonia (NH) in the water column is:

$$\frac{d(NH_w)}{dt} = -\sum_{i=PX_w} P_{NH_w,i} - P_{NH_w,MB_w} - P_{NH_w,MA} - P_{NH_w,PFB} + \sum_{i=CX_w,\,BF} E_i + \sum_{i=FX} E_i + \sum_{\substack{i=\text{pelagic} \\ \text{bacteria}}} E_i - S_{NIT,PAB} + R_{NET,w} \quad \text{(C.12)}$$

and in the sediment:

$$\frac{d(NH_{sed})}{dt} = R_{NET,sed} - S_{NIT,sed} - P_{NH_{sed},MB_{sed}} - P_{NH_{sed},SG} + \sum_{i \neq BF,CX_w} E_i \quad \text{(C.13)}$$

where $P_{NH,XX}$ is the uptake of NH by the autroph XX, E_{CX} is the production of NH by the consumer CX, $S_{NIT,XB}$ is the amount of NH lost due to nitrification by the bacteria

XB, R_{NET} is the amount of NH produced by denitrification.

The rates of change for nitrate (NO) in the water column is given by:

$$\frac{d(NO_w)}{dt} = -\sum_{i=PX_w} P_{NO_w,i} - P_{NO_w,MB_w} - P_{NO_w,MA} + S_{NIT,PAB} \quad \text{(C.14)}$$

and in the sediment:

$$\frac{d(NO_{sed})}{dt} = S_{NIT,sed} - S_{DENIT,sed} - P_{NO_{sed},MB_{sed}} - P_{NO_{sed},SG} \quad \text{(C.15)}$$

The rates of change of dissolved silicate (Si) in the water column is:

$$\frac{d(Si_w)}{dt} = R_{DSisol,w} - \sum_{i=PL_w,MB_w} P_{Si_w,i} \quad \text{(C.16)}$$

and the rate of change of detrital silica (DSi) in the water column is given by:

$$\frac{d(DSi_w)}{dt} = X_{SiN}\left(\sum_{i=PL_w,MB_w}\left(M_{lys,i} + \sum_{j=CX_w} P_{i,j}\right)\right) - R_{DSisol,w} \quad \text{(C.17)}$$

where X_{SiN} is the Redfield ratio of silicon and nitrogen (set at 3.0 (Murray and Parslow 1997)) and R_{DSisol} is the amount of detrital silica remineralised. Note that the equations for Si_{sed} and DSi_{sed} are as for (C.16) and (C.17) except that CX_{sed} is used in the place of CX_w and MB is the only PX present in the sediment that uses Si.

The rates of change for dissolved oxygen (O2) in the water column is given by:

$$\frac{d(O2_w)}{dt} = X_{ON}\left(\sum_{i=PX_w} G_i + G_{MB_w} + G_{MA} + \frac{G_{SG}}{2} - \sum_{\substack{i\neq infauna,\\ MZ,BG}} E_i - \sum_{i=FX} E_i - \sum_{\substack{i=pelagic\\ bacteria}} E_i - R_{DON,w}\right) \quad \text{(C.18)}$$

and in the sediment:

$$\frac{d(O2_{sed})}{dt} = X_{ON}\left(G_{MB_{sed}} + \frac{G_{SG}}{2} - \sum_{\substack{i=infauna,\\ MZ,BG}} E_i - R_{DON,sed}\right) \quad \text{(C.19)}$$

where X_{ON} is the Redfield ratio of oxygen and nitrogen (set at 16.0 (Murray and

Parslow 1997)) and R_{DON} is the DON lost due to remineralisation.

The rates of change of dissolved organic nitrogen (DON) in the water column is:

$$\frac{d(DON_w)}{dt} = W_{DON,w} - R_{DON,w} - P_{DON,PFB} \quad \text{(C.20)}$$

and in the sediment:

$$\frac{d(DON_{sed})}{dt} = W_{DON,sed} - R_{DON,sed} \quad \text{(C.21)}$$

where W_{DON} is the DON produced by bacteria, R_{DON} is the DON lost due to remineralisation and $P_{DON,PFB}$ is the DON taken up by pelagic free bacteria (PFB).

The rates of change of labile detritus (DL) in the water column is:

$$\frac{d(DL_w)}{dt} = \sum_{i=CX_w} W_{DL_w,i} + \sum_{i=FX} W_{DL_w,i} + \sum_{\substack{i=\text{pelagic} \\ \text{bacteria}}} W_{DL_w,i} + \sum_{i=PX_w} M_{lys,i} + M_{lys,MB_w} + M_{MA} - P_{DL_w,PAB} - P_{DL_w,BF} \quad \text{(C.22)}$$

and in the sediment:

$$\frac{d(DL_{sed})}{dt} = \sum_{i=PX_{sed}} M_{nat,i} + M_{nat,MB_{sed}} + M_{lys,MB_{sed}} + M_{SG} + \sum_{i=infauna} (W_{DL,i} - P_{DL_{sed},i}) + \sum_{i=epifauna} (W_{DL,i} - P_{DL_{sed},i}) - \sum_{i=FX} P_{DL_{sed},i} \quad \text{(C.23)}$$

where $W_{DL,CX}$ is the amount of DL in the waste products from consumer CX and $P_{DL,CX}$ is the DL consumed by CX.

The rates of change of refractory detritus (DR) in the water column is given by:

$$\frac{d(DR_w)}{dt} = \sum_{i=FX} W_{DR_w,i} - \sum_{i=CX_w} P_{DR_w,i} - P_{DR_w,PAB} - J_{DR} \quad \text{(C.24)}$$

and in the sediment:

$$\frac{d(DR_{sed})}{dt} = \sum_{i=infauna} W_{DR_{sed},i} - \sum_{i=infauna} P_{DR_{sed},i} + J_{DR} \quad \text{(C.25)}$$

where $W_{DR,CX}$ is the DR in the wastes of consumer CX, $P_{DR,CX}$ is the amount of detritus

consumed by CX, infauna includes sediment bacteria and J_{DR} is the amount of DR transferred from the water column to sediment pool due to the feeding activities of the benthic filter feeders.

C.2 Process equations

Growth of primary producers

$$G_{PX} = \mu_{PX} \cdot \delta_{irr} \cdot \delta_{N} \cdot \delta_{space} \cdot PX \tag{C.26}$$

with μ_{PX} is the maximum growth rate, the nutrient limitation factor due to nitrogen is given by:

$$\delta_{N} = \frac{DIN}{\kappa_{N,PX} + DIN} \tag{C.27}$$

(where DIN=NH+NO) except for those primary producers which are also limited by the availability of Si then nutrient limitation is given by:

$$\delta_{N} = min\left(\frac{DIN}{\kappa_{N,PX} + DIN}, \frac{Si}{\kappa_{Si,PX} + Si}\right) \tag{C.28}$$

and light limitation is given by:

$$\delta_{irr} = min\left(\frac{IRR}{\kappa_{irr,PX}}, 1\right) \tag{C.29}$$

with the κ representing the half saturation constants for the respective processes, and space limitation as follows:

$$\delta_{space} = 1 - \frac{PX}{\theta_{PXmax}} \tag{C.30}$$

Using the above formulations for growth and nutrient limitation the nutrient uptake functions for the primary producer PX are given by:

$$P_{NH,PX} = G_{PX} \cdot \frac{NH}{\kappa_{NH,PX} + NH} \cdot \frac{\kappa_{NH,PX} + DIN}{DIN} \tag{C.31}$$

$$P_{NO,PX} = G_{PX} \cdot \frac{NO}{DIN} \cdot \frac{\kappa_{NH,PX}}{\kappa_{NH,PX} + NH} \qquad \text{(C.32)}$$

where $\kappa_{NH,PX}$ is the half saturation constant for the uptake of NH. In addition, for PL and MB there is the uptake of Si as follows:

$$P_{Si,PX} = X_{SiN} \cdot G_{PX} \qquad \text{(C.33)}$$

Growth of consumers

The growth of an invertebrate consumer (CX) is given by:

$$G_{CX} = \left(\varepsilon_{CX} \cdot \sum_{\substack{i=\text{living} \\ \text{prey}}} P_{i,CX} + \sum_{j=DL,DR} \left(P_{j,CX} \cdot \varepsilon_{CX,j} \right) \right) \cdot \delta_{space} \cdot \delta_{o2} \qquad \text{(C.34)}$$

with ε_{CX} the growth efficiency of CX when feeding on live prey, $\varepsilon_{CX,j}$ the efficiency when feeding on detritus (DL treated separately to DR), space limitation given by:

$$\delta_{space} = \begin{cases} 1 - \dfrac{(CX - \theta_{CXlow}) \cdot \frac{(CX - \theta_{CXlow})}{CX - \theta_{CXlow} + \kappa_{CXsat}}}{(CX - \theta_{CXlow}) \cdot \frac{(CX - \theta_{CXlow})}{CX - \theta_{CXlow} + \theta_{CXsat}} + \kappa_{CXthresh}} & , \quad CX = \text{BF and } CX > \theta_{CXlow} \\ 1 & , \quad \text{otherwise} \end{cases} \qquad \text{(C.35)}$$

where θ_{CXmax} is the maximum biomass per area allowed for CX, θ_{CXlow} is the crowding lower threshold, κ_{CXsat} is the crowding half saturation level, and $\kappa_{CXthresh}$ is the crowding threshold (this formulation is based on that of the European Regional Seas Ecosystem Model II (ERSEM II) (Blackford 1997)). The oxygen limitation in the standard runs of BM2 is given by:

$$\text{or } \delta_{o2} = \begin{cases} \dfrac{\gamma_{o2}}{\gamma_{o2} + \kappa_{CX,Mo2}} & , \text{if epifauna or infauna} \\ 1 & , \text{if pelagic} \end{cases} \qquad \text{(C.36)}$$

where γ_{o2} is the depth of the oxygen horizon and $\kappa_{CX,Mo2}$ is the half oxygen mortality depth.

The growth for each fish group, is calculated by equation of the same form as

(C.34), but per age group of each fish, the result is then apportioned to structural and reserve weight increases such that:

$$G_{FX_{i,s}} = \Lambda \cdot G_{FX_i} \tag{C.37}$$

$$G_{FX_{i,r}} = (1-\Lambda) \cdot G_{FX_i} \tag{C.38}$$

where

$$\Lambda = \begin{cases} \dfrac{\frac{1}{X_{RS}} + X_{pR,FX} \cdot \left(-\frac{FX_{i,r}}{X_{RS} \cdot FX_{i,s}}\right)}{\frac{1}{X_{RS}} + \cdot \frac{FX_{i,r}}{X_{RS} \cdot FX_{i,s}}}, & \text{if} > 0 \text{ and } G_{FX_i} > 0 \\ = 0 & \text{, otherwise} \end{cases} \tag{C.39}$$

with X_{RS} the maximum ratio of reserve to structural weight FX can have and $X_{pR,FX}$ is the relative degree to which FX concentrates on replenishing reserves rather than undergoing structural growth when underweight.

In the standard form of BM2 presented here the grazing term is given by:

$$P_{prey,CX} = \frac{CX \cdot k_{CX} \cdot p_{prey,CX} \cdot prey}{1 + k_{CX} \cdot \frac{\varepsilon_{CX} \cdot \left(\sum_{\substack{j=\text{live prey} \\ \text{groups}}} p_{j,CX} \cdot j\right) + \varepsilon_{CX,DL} \cdot p_{DL,CX} + \varepsilon_{CX,DR} \cdot p_{DR,CX}}{\mu_{CX}}} \tag{C.40}$$

where "prey" is the group being consumed by CX, k_{CX} is the clearance rate of CX and $p_{prey,CX}$ is preference (or availability) of that prey for the predator CX. This last parameter is similar to the "vulnerability" parameters in ECOSIM (Christensen et al. 2000) and represents the fact that the entire prey population will not be available to the predators at any one time (some may be hiding for instance). The availability of the food is further modified if the spatial range of the predator and prey do not completely overlap (and so explicit spatial refuges exist). The available fish in cohort i of fish group FX (FX_i), for the fish eating cohorts of piscivorous (FV) and demersal (FD) fish (FY_j), is given by:

$$A_{FX_i} = \begin{cases} \Sigma p_{FXi,FYj} \cdot \frac{(FX_{i,s} + FX_{i,r}) * FX_{i,d}}{cell\_vol}, & \Theta_{low,FY} \cdot FY_{j,s} \le FX_{s,i} \le \Theta_{up,FY} \cdot FY_{j,s} \\ 0 & \text{, otherwise} \end{cases} \tag{C.41}$$

where $\Theta_{low,FY}$ is the lower prey selection size limit for FY and $\Theta_{up,FY}$ is the upper prey selection size limit. The availability of benthic prey to their predators (fish and invertebrate alike) is calculated in a slightly different way and is as follows:

$$A_{prey} = prey \cdot d_{prey} \tag{C.42}$$

where, if aerobic

$$d_{prey} = \begin{cases} 0 & , \gamma_{CX} < \gamma_{top} \\ \frac{(\gamma_{CX} - \gamma_{top})}{(\gamma_{o2} - \gamma_{top})} & , \gamma_{top} < \gamma_{CX} < \gamma_{o2} \\ 1 & , \gamma_{top} < \gamma_{o2} < \gamma_{CX} \end{cases} \tag{C.43}$$

and if anaerobic

$$d_{prey} = \begin{cases} 1 & , \gamma_{CX} < \gamma_{top} \\ \left(1 - \frac{(\gamma_{CX} - \gamma_{top})}{(\gamma_{o2} - \gamma_{top})}\right) & , \gamma_{top} < \gamma_{CX} < \gamma_{o2} \\ 0 & , \gamma_{top} < \gamma_{o2} < \gamma_{CX} \end{cases} \tag{C.44}$$

where γ_{CX} is the depth in the sediment that the predator CX can forage down to and γ_{top} is set to zero for all standard runs (as there is only one sediment layer).

Mortality and loss functions

The mortality terms for invertebrate consumers and autotrophs are in terms of lost biomass while those for fish refer to the number of individuals lost. Nevertheless the general form of the equations is the same (but the units of the coefficients obviously differ between the fish and other groups). The natural mortality term for group XX is given by

$$M_{XX} = m_{lin,XX} \cdot XX + m_{quad,XX} \cdot XX^2 + (1 - \delta_{o2}) \cdot m_{o2,XX} \cdot XX + m_{special,XX} \cdot XX + m_{top,XX} \cdot XX \tag{C.45}$$

where $m_{lin,XX}$ is the coefficient of linear mortality for XX, $m_{quad,XX}$ is the coefficient of quadratic mortality for the group XX, $m_{O2,XX}$ is the coefficient of oxygen dependent mortality and $m_{special,XX}$ is the special (additional) loss rate for XX. This rate of "special"

mortality is usually set to zero, except in the following cases:

$$m_{special,MA} = STRESS \cdot m_{STRESS} \quad \text{(C.46)}$$

$$m_{special,SG} = DIN \cdot m_{DIN} \quad \text{(C.47)}$$

where m_{STRESS} and m_{DIN} are the coefficient of mortality due to mechanical stress and fouling by epiphytes, respectively. Lastly:

$$m_{special,FX_i} = \begin{cases} \dfrac{m_{starve,FX} \cdot \theta_{starve} \cdot (1 + X_{RS}) \cdot FX_{i,s} - (FX_{i,s} + FX_{i,r})}{(1 + X_{RS}) \cdot FX_{i,s}} & \text{, if } > 0 \\ = 0 & \text{, otherwise} \end{cases} \quad \text{(C.48)}$$

with $m_{starve,FX}$ is the threshold ratio of reserve to structural weight at which death due to starvation is likely. The final term of equation (C.45) was adopted from ERSEM I (Bryant et al. 1995) to represent the impact of seabirds and other top predators and is given by:

$$m_{top,XX} = m_{seabird,XX} + m_{shark,XX} \quad \text{(C.49)}$$

While all the groups in the standard run of the model had a linear mortality term, some groups (the fish and higher trophic level zooplankton and benthic groups) suffered mortality described by a quadratic term. Only benthic consumers had oxygen dependent mortality, the macrophyte and fish groups had special mortality as shown above and m_{top} is only applied to the fish groups.

Fishing is another process that is only applied to fish in the standard runs. The amount caught at time t is given by:

$$F_{FX,t} = C_{eff} \cdot (FX_{s,i} + FX_{r,i}) \cdot FX_{di,} \cdot q_{FX_i} \quad \text{(C.50)}$$

where q_{FXi} is the catchability of the ith age group of FX and

$$C_{eff} = \begin{cases} m_{FC,FX} & \text{, standard runs} \\ \dfrac{m_{FCmax,FX}}{1 + e^{(-m_{FCa} \cdot F_{FX_i,t-1})}} & \text{, effort model on} \end{cases} \quad \text{(C.51)}$$

with $m_{FC,FX}$ the coefficient of fishing mortality for FX, $m_{Fcmax,FX}$ the maximum fishing

mortality allowed for FX and $m_{Fca,FX}$ the coefficient of spread for the fishing mortality of FX. As indicated by (C.50) and (C.51) the fishing implemented for standard runs is a simple catch equation.

The final loss term is one that is applied to the microscopic primary producers only and it represents lysis. The losses of a primary producer (PX) to lysis is formulated as follows:

$$M_{lys,PX} = \frac{m_{lys,PX} \cdot PX}{\delta_N + 0.1} \qquad \text{(C.52)}$$

with $m_{lys,PX}$ the rate of lysis.

Waste processes

The production of waste products by invertebrate consumers and fish are handled in the same way, but in the case of fish the mortality term has to be converted from a density to a biomass before being used in the following equations. The production of labile detritus (DL) by consumer group XX is given by:

$$W_{DL} = \left(\begin{array}{l} (1-\varepsilon_{XX}) \cdot \Gamma_{XX} \cdot \sum_{\substack{i=\text{living prey} \\ \text{group}}} P_{i,XX} + (1-\varepsilon_{XX,DL}) \cdot \Gamma_{XX,DL} \cdot P_{DL,XX} \\ + (1-\varepsilon_{XX,DR}) \cdot \Gamma_{XX,DR} \cdot P_{DR,XX} + \varphi_{XX} \cdot M_{XX} \end{array} \right) \cdot f_{XX,DL} \qquad \text{(C.53)}$$

with φ_{XX} the proportion of mortality losses assigned to detritus, Γ_{XX} the proportion of the growth inefficiency of XX when feeding on live prey that is sent to detritus, $\Gamma_{XX,DL}$ the proportion of the growth inefficiency of XX when feeding on DL that is sent to detritus, $\Gamma_{XX,DR}$ the proportion of the growth inefficiency of XX when feeding on refractory detritus (DR) that is sent to detritus and $f_{XX,DL}$ is the proportion of the total detritus produced that is of the type DL. The same equation is used for the production of DR (W_{DR}), except that the final multiplication of the brackets by $f_{XX,DL}$ is replaced by multiplication by $(1-f_{XX,DL})$.

The other main waste product is excreted ammonia. The general formulation

used for the production of ammonia by a consumer XX (invertebrate or fish) is as follows:

$$E_{XX} = (1-\varphi_{XX})\cdot M_{XX} + (1-\varepsilon_{XX})\cdot(1-\Gamma_{XX})\cdot \sum_{\substack{i=\text{living prey}\\ \text{group}}} P_{i,XX} + (1-\varepsilon_{XX,DL})\cdot(1-\Gamma_{XX,DL})\cdot P_{DL,XX} + (1-\varepsilon_{XX,DR})\cdot(1-\Gamma_{XX,DR})\cdot P_{DR,XX} \quad \text{(C.54)}$$

Physical processes

The only physical processes in BM2 that differ from those in the Port Phillip Bay Integrated Model (detailed in Murray and Parslow 1997, Walker 1997) are bioturbation, bioirrigation (detailed in the main text of chapters 1 and 2) and the calculation of the light attenuation coefficient. The formulation of the coefficient used in the Integrated Generic Bay Ecosystem Model (IGBEM) is adopted in BM2 and it is an expanded form of the one used in PPBIM. The coefficient is given by:

$$n = n_w + n_{DON}\cdot DON + n_D\cdot(DL+DR) + n_P\cdot\sum_{i=PX} PX + n_{susp}\cdot SUSP \quad \text{(C.55)}$$

with n_w the background extinction coefficient, n_{DON} the contribution due to DON, n_D the contribution due to detritus, n_P the contribution due to phytoplankton (PX) and n_{susp} the contribution due to suspended sediments (SUSP).

Appendix D: Equations for dinoflagellates and mixotrophy in Bay

Model 2

Note: For quick reference, a list of the main terms used in the equations in this appendix is given in Appendix B, Table B.3.

The formulation for the rate of change of dinoflagellates is:

$$\frac{d(DF)}{dt} = G_{DF} - M_{DF} - \sum_{i=DF,ZL} P_{DF,i} \qquad (D.1)$$

where M_{DF} describes losses due to lysis suffered by the dinoflagellate pool (DF); $P_{DF,i}$ are predation losses suffered by the dinoflagellate pool; and the total growth (G_{DF}) is given by

$$G_{DF} = G_{phs,DF} + \varepsilon_{DF} \cdot G_{phag,DF} \qquad (D.2)$$

where photosynthetic growth ($G_{phs,DF}$) is given by

$$G_{phs,DF} = \mu_{DF} \cdot \delta_{irr} \cdot \delta_{N} \cdot DF \qquad (D.3)$$

while the phagotrophic contribution ($G_{phag,DF}$) to total growth is given by

$$G_{phag,DF} = \mathit{min}\left(\sum_{\text{prey groups}} P_{i,DF} \;,\; \frac{\mu_{DF}}{\varepsilon_{DF}} \cdot \delta_{irr} \cdot (1-\delta_{N}) \cdot DF \right) \qquad (D.4)$$

ε_{DF} is the assimilation efficiency of the mixotrophic dinoflagellates (set at 0.6); μ_{DF} is the temperature dependent maximum daily growth rate of the dinoflagellates (set at 0.5 mg N d^{-1}, Murray pers. com.), δ_{irr} is the light limitation factor, δ_{N} the nutrient limitation factor and $P_{i,DF}$ the amount of prey group i grazed by the predator DF, which is calculated in the same way as for all other grazers in BM2. The light and nutrient limitation factors were largely calculated as for the pure autotrophs in BM2. Since there is strong evidence that dinoflagellates show an increase in efficiency at low light levels (Jeong et al. 1999, Li et al. 1999), there were some modifications made to the formulation of light limitation for this group. The modification is based on general

observations that, due to increased efficiency at low light levels, mixotrophic growth rates are two- to three-fold higher than those of strict phototrophic growth under identical (low light) conditions (Skovgaard 1996, Legrand et al. 1998, Li et al. 1999). The final form of the light limitation factor (δ_{irr}) is:

$$\delta_{irr} = \begin{cases} \min(IRR \cdot 0.01 + 0.018, 1), & 0 < IRR \leq 0.1 \\ \min\left(\frac{IRR}{\kappa_{irr,DF}}, 1\right), & \text{otherwise} \end{cases} \quad \text{(D.5)}$$

and the nutrient limitation factor as

$$\delta_N = \frac{DIN}{\kappa_{N,DF} + DIN} \quad \text{(D.6)}$$

where *DIN* represents the total inorganic nitrogen pool (made up of ammonia and nitrate).

Appendix E: Equations for bacteria and sediment chemistry in Bay

Model 2

Note: For quick reference, a list of the main terms used in the equations in this appendix is given in Appendix B, Table B.3.

The general formulation for the dynamics of aerobic attached bacteria (where *XB* stands for Pelagic Attached Bacteria (PAB) or sediment bound Aerobic Bacteria (AEB)) is:

$$\frac{d(XB)}{dt} = G_{XB} - M_{XB} - \sum_{\substack{\text{i=consumer} \\ \text{groups}}} P_{XB,i} \qquad \text{(E.1)}$$

where the growth of the group of bacteria (G_{XB}) is given by

$$G_{XB} = \mu_{XB} \cdot XB \cdot max\left(0, (1-\rho_{XB})^{\psi}\right) \qquad \text{(E.2)}$$

and

$$\rho_{XB} = \frac{XB}{\left(\tau_{DL,XB} \cdot DL + \tau_{DR,XB} \cdot DR\right) \cdot \delta_{O2} \cdot \delta_{stim}} \qquad \text{(E.3)}$$

with μ_{XB} representing the maximum temperature-dependent daily growth rate for the group XB. *XB* is the current pool of bacteria and *DL* and *DR* are the labile and refractory detrital pools (all in mg N m^{-3}); $\tau_{DL,\,XB}$ and $\tau_{DR,\,XB}$ represent the maximum possible biomass of XB per biomass of that grade of detritus; ψ is the exponent dictating the reduction in growth as the bacterial pool approaches its maximum attainable levels (set to 3 in all standard runs) and δ_{O2} is the oxygen limitation factor, which is given by:

$$\delta_{O2} = \begin{cases} \dfrac{\gamma_{O2}}{\gamma_{O2} + \gamma_{XB}}, & \text{XB benthic} \\ 1, & \text{otherwise} \end{cases} \qquad \text{(E.4)}$$

where γ_{XB} is the half oxygen mortality depth for XB, and the oxygen horizon (γ_{O2}) is given by:

$$\gamma_{O2} = \frac{2 \cdot O2_{sed} \cdot \gamma_{sed}}{O2_{bw}} \qquad \text{(E.5)}$$

with $O2_{sed}$ the concentration of oxygen in the sediments, $O2_{bw}$ the concentration in the bottom water and γ_{sed} the depth of the sediment layer considered in the model. Finally δ_{stim} indicates the degree of stimulation of the bacteria by bioturbation and it is calculated as follows:

$$\delta_{stim} = \begin{cases} \dfrac{\delta_{te} \cdot 250 \cdot (POR\text{-}0.225)}{193.75}, & \text{XB benthic} \\ 1, & \text{otherwise} \end{cases} \qquad \text{(E.6)}$$

Use of a compound effect of enhanced bioturbation (δ_{te} calculated in the same way as for IGBEM – chapter 1), and porosity (POR) is based on observations by Alongi (1998) and the relationship detailed by Blackburn (1987). Using equations (E.2) to (E.5), the utilisation of labile detritus by aerobic bacteria is given by:

$$P_{DL,XB} = G_{XB} \cdot \frac{\rho_{XB} \cdot \tau_{XB,DL} \cdot DL}{XB \cdot \varepsilon_{XB,DL}} \qquad \text{(E.7)}$$

where $\varepsilon_{XB,DL}$ is the assimilation efficiency of the bacteria on labile detritus. The uptake of refractory detritus is calculated similarly. The natural mortality term (M_{XB}) is as for the other invertebrates (Appendix B), but the term representing predation losses to predator group i ($P_{XB,i}$) is given by:

$$P_{XB,i} = P_{DL,i} \cdot \rho_{XB} \cdot \tau_{XB,DL} + P_{DR,i} \cdot \rho_{XB} \cdot \tau_{XB,DR} \qquad \text{(E.8)}$$

The waste handling equations for bacteria are also different to those for other invertebrates since wastes are channelled into DON not DL. All of the equations for the Anaerobic Bacteria (ANB) are as for XB here, except that any δ_{O2} factors in the equations are replaced by $(1\text{-}\delta_{O2})$. Adopting these equations for the attached bacteria made it easier to identify a method of introducing dynamic flexibility to the empirical nitrification-denitrification model proposed by Murray and Parslow (1999a) for PPBIM.

To integrate a more interactive form of the processes governing nitrification and

denitrification into BM2, the empirical sediment chemistry model used in PPBIM (Murray and Parslow 1999a) is linked directly to the activities of sediment bacteria and infauna. The amount of ammonia produced by the remineralisation of DON (R_{DON}) is handled as in PPBIM, that is:

$$R_{DON} = \Phi \cdot DON \cdot POR \qquad \text{(E.9)}$$

where Φ is the temperature-dependent rate of breakdown for DON (set at 0.00176 d^{-1}, Murray pers. com.). In PPBIM, equations similar to (E.9) were used to calculate the production of ammonia due to the breakdown of DL and DR (Murray and Parslow 1997). This is not the case in BM2, where the production of the remainder of the ammonia is dependent upon the activity of sediment dwelling fauna and flora. Thus, the total ammonia available for nitrification and denitrification (R_{NET}) is:

$$R_{NET} = \boldsymbol{max}\left(0, R_{DON} + E_{AEB} + E_{ANB} + \xi \cdot \left(E_{OB} + E_{BD}\right) - P_{NH,MB}\right) \qquad \text{(E.10)}$$

where $P_{NH,MB}$ is the uptake of NH by MB (see equations for autotrophs in Appendix C), E_{XX} is the ammonia released by XX and ξ is the fraction of the excreted NH by infauna that contributes available nitrogen for nitrification and denitrification (set to 0.95 in the standard runs). The form of E_{XX} for OB and BD is of the general form given for heterotrophs in Appendix B, but that for AEB and ANB is slightly different and is given by:

$$E_{XB} = P_{DL,XB} \cdot \left(1 - \varepsilon_{XB,DL}\right) + P_{DR,XB} \cdot \left(1 - \varepsilon_{XB,DR}\right) + M_{XB} - W_{DON} - W_{DR} \qquad \text{(E.11)}$$

where E_{XB} is the release of NH by XB, $\varepsilon_{XB,DX}$ is the efficiency of XB on the detritus fraction DX, and the production of DON (W_{DON}) and DR (W_{DR}) are calculated as follows:

$$W_{DON} = \left(P_{DL,XB} \cdot \left(1 - \varepsilon_{XB,DL}\right) + P_{DR,XB} \cdot \left(1 - \varepsilon_{XB,DR}\right) + M_{XB} \cdot \varphi_{XB}\right) \cdot f_{XB,DON} \qquad \text{(E.12)}$$

$$W_{DR} = \left(P_{DL,XB} \cdot \left(1 - \varepsilon_{XB,DL}\right) + M_{XB} \cdot \varphi_{XB}\right) \cdot f_{XB,DR} \qquad \text{(E.13)}$$

where φ_{XB} indicates the fraction of the losses of XB due to natural mortality that are not

released as NH and $f_{XB,DX}$ is the fraction of the products of growth inefficiency and mortality directed to the detritus fraction DX. Using equation (E.10) the processes of nitrification and denitrification were completed using the form of the empirical model of Murray and Parslow (1999a), giving nitrification (S_{NIT}) as:

$$S_{NIT} = R_{NET} \cdot \theta_{DMAX} \cdot \boldsymbol{max}\left(0, 1 - \frac{R_{NET} \cdot \gamma_{SED}}{r0}\right) \quad \text{(E.14)}$$

and denitrification (S_{DENIT}) as:

$$S_{DENIT} = S_{NIT} \cdot \boldsymbol{min}\left(1, \frac{R_{NET} \cdot \gamma_{SED}}{\theta_{rD}}\right) \quad \text{(E.15)}$$

where θ_{DMAX} is the maximum rate of denitrification (set at 0.25, Murray pers. com.), θ_{r0} is the temperature-dependent minimum rate of respiration that supports nitrification (set at 200, Murray and Parslow 1997) and θ_{rD} (set at 10, Murray and Parslow 1997) is the peak of the nitrification-denitrification curve (as defined by Murray and Parslow 1999a). This general form is adopted from PPBIM due to its demonstrated performance and robustness (Murray and Parslow 1999a, chapter 1).

The more interactive representation of sediment processes lead to a minor modification to the bioirrigation equations. The formulation remained unchanged from that of PPBIM (Walker 1997) and IGBEM (chapter 1) for the majority of groups, but for oxygen it became:

$$O2_{bw,t+1} = \frac{\left(O2_{bw,t} \cdot VOL_{bw} + O2_{sed,t} \cdot VOL_{por}\right)}{VOL_{bw} + VOL_{por}} + e^{-\phi_{irr}\left(\frac{1}{VOL_{bw}} + \frac{1}{VOL_{por}}\right)} \cdot \left(O2_{bw,t} - \frac{\left(O2_{bw,t} \cdot VOL_{bw} + O2_{sed,t} \cdot VOL_{por}\right)}{VOL_{bw} + VOL_{por}}\right) \quad \text{(E.16)}$$

$$O2_{sed,t+1} = O2_{sed,t} - \frac{VOL_{bw}}{VOL_{por}} \cdot \left(O2_{bw,t+1} - O2_{bw,t}\right) \quad \text{(E.17)}$$

where ϖ_{irr} is the exchange rate due to irrigation (calculated as for IGBEM (chapter 1)),

$O2_{SED,t}$ is the concentration of oxygen in the sediment at time t, $O2_{bw,t}$ is the concentration of oxygen in the bottom water at time t, VOL_{bw} is the volume of the bottom water layer and the porewater volume above the oxygen horizon is given by:

$$VOL_{por} = POR \cdot \frac{\gamma_{o2} \cdot \chi_{cell}}{VOL_{sed}} \qquad \text{(E.18)}$$

with VOL_{sed} being the volume of the entire sediment layer and χ_{cell} is the area of the cell. All other parts of the transport model were as implemented in IGBEM (chapter 1).

Appendix F: Equations for fish movement in Bay Model 2

Note: For quick reference, a list of the main terms used in the equations in this appendix is given in Appendix B, Table B.3.

Fish movement (in terms of the density d of fish group FX, age class i, in cell j) in the standard set-up of BM2 is given by:

$$FX_{i,d,j} = \begin{cases} FX_{i,tot} \cdot \left(\vartheta \cdot \left(\mathbf{FDEN}_{j,qrt+1,FX} - \mathbf{FDEN}_{j,qrt,FX}\right) + \mathbf{FDEN}_{j,qrt,FX}\right), & qrt < 4 \\ FX_{i,tot} \cdot \left(\vartheta \cdot \left(\mathbf{FDEN}_{j,1,FX} - \mathbf{FDEN}_{j,qrt,FX}\right) + \mathbf{FDEN}_{j,qrt,FX}\right), & qrt = 4 \end{cases} \quad \text{(F.1)}$$

where $FX_{i,tot}$ is the total number of FX in age class i in the entire system (that is the sum over all cells), ϑ is the proportion of the current quarter of the year which has already passed, $\mathbf{FDEN}_{j,qrt,FX}$ is the proportion of the population of FX found in cell j in the qrt quarter of the year.

For the forage and density dependent fish movement scheme, the following formulation is used:

$$G_{FX,i,j,potential} = \begin{cases} g_{roc\_mult} \cdot G_{FX,i,j}, & G_{FX,i,j} > g_{thesh} \\ \dfrac{G_{FX,i,j}}{g_{roc\_mult}}, & \text{otherwise} \end{cases} \quad \text{(F.2)}$$

$$G_{FX,i,tot} = \sum_{\text{all } j} G_{FX,i,j} \quad \text{(F.3)}$$

$$FX_{i,d,j} = \frac{FX_{i,tot} \cdot G_{FX,i,j,potential}}{G_{FX,i,tot}} \quad \text{(F.4)}$$

where $G_{FX,i,j,potential}$ is a measure of the potential attractiveness of the cell j based on the available forage, $G_{FX,i,j}$ is calculated as of G_{CX} in equation C.34, g_{roc_mult} is a constant reflecting how much more attractive a sight with forage sufficient to support FX_i is over a site with poor food resources and g_{thresh} is the potential growth rate (as an index of the quality of the resources) where FX_i switch from finding the site desirable to undesirable.